EVOLUTION OF THE EARLIEST SMOOTH SPIRE-BEARING ATRYPOIDS (BRACHIOPODA: LISSATRYPIDAE, ORDOVICIAN–SILURIAN)

by PAUL COPPER

ABSTRACT. Calcified lophophore supports present in the oldest of the spire-bearing brachiopods, the Lissatrypidae which range in age from middle Ordovician (Caradoc) through middle Silurian (Wenlock) time, demonstrate complex evolutionary patterns and early divergence. The smooth-shelled brachiopods *Protozyga*, *Idiospira*, and *Cyclospira*, which had medially or dorso-medially directed spiralia, evolved from the primitive early Caradoc atrypoid *Manespira* n. gen., which had a spiralium of less than one whorl and a whole or partial jugum. Early divergence produced four separate lineages, the Protozyginae n. subfam., Septatrypinae, Cyclospirinae, and Zygospiridae (which led to the ribbed atrypoids). Each of these groups developed distinctive brachidia, probably a reflection of early experimentation in filter-feeding strategies. In late Ordovician and early Silurian time, the ribbed Atrypidae, which had evolved from the Zygospiridae, expanded rapidly to dominate the shallow benthos of tropical seas: they accomplished this by perfecting large shell sizes, increasing the number of whorls in the spiralia, orienting the spiralia dorsally and separating the jugum into discrete processes. The smooth-shelled atrypoids, Lissatrypidae, usually played a secondary role, though they were prominent in the Silurian. Two new developments took place in the Silurian: evolution of the thicker-shelled Lissatrypinae (by mid-Llandovery), and the unique Glassiinae, with medially directed spiralia (by Wenlock time). Both of these declined during the Devonian, but the Glassiinae were the last survivors of the smooth atrypoids in late Devonian (Frasnian) time, with a new genus, *Peratos* (type species *P. arrectus* n. sp.), ending the lineage.

SOME one hundred years ago Thomas Davidson (1881*a*) suggested that there were only four spire-bearing brachiopod families: these were based on the common genera *Spirifer*, *Athyris*, *Nucleospira*, and *Atrypa*. Except for the Nucleospiridae, which are now submerged within the family Athyridae, Davidson's categories have stood the century test of time very well, even though the families now have higher taxonomic rank. The Treatise (Boucot *et al.* 1965) has broadly treated the spire-bearing brachiopods as a monophyletic stock under the order Spiriferida. With the discovery of dorsally directed spiralia in the 'orthid' *Tuvaella* by Vladimirskaya (1972), in the 'strophomenid' *Davidsonia* by Garcia-Alcalde (1973) and Copper (1978), and in the 'rhynchonellid' *Hircinisca* by Havlicek and Plodowski (1974), the Tuvaellidae and at least some Davidsoniidae and 'rhynchonellids' may be further added to the spire-bearers. Rzhonsnitskaya (1960), Rudwick (1970), and more recently Wright (1979), have supported a diphyletic view of the spire-bearers, with the Spiriferidae derived from an orthid stock during the late Ashgill or early Llandovery and the Atrypida (including, for these authors, the *Atrypa* and *Athyris* groups) evolving from rhynchonellids during Llandeilo time. This paper is an attempt to clarify the basic internal structures, particularly the brachidia (crura, jugum, and spiralia) which supported the lophophore, of the earliest smooth spire-bearing brachiopods. It is a follow-up of an earlier paper (Copper 1977) which dealt with the oldest ribbed spire-bearers, the Zygospiridae.

The information on which this paper is based is the re-examination of all types and topotypes of the known Ordovician and most of the Silurian type species of smooth atrypoid spire-bearing genera, i.e. those with medially or dorsally directed spiralia. Reconstructions of the internal morphology are based on the technique of serial sectioning using rapid-drying 0·004 mm thick, Acetobutyratfolie peels (made by Bayer G. m. b. H., Leverkusen, Germany). These peels were mounted under glass

and projected with standard 35 mm slide projectors on white paper, and then copied on tracing paper. Peel details are of high resolution and can be photographed under a microscope. The traced images were then measured into the plane parallel to the shell commissure (or at right angles to the angle of sectioning) using the plane of bilateral symmetry as a guide. A ventral three-dimensional view of the brachial valve and the brachidia was then reconstructed by tracking points from the section plane into the commissural plane (technique developed by Copper 1967). Lateral view reconstructions were also made, using the curve of the plane of symmetry of the brachial valve as the base line (using plaster casts of the sectioned specimens), and normally drawing only the right spiralium as viewed into the dorsal valve. Such reconstructions are accurate to 0·5 mm at a magnification of × 12, × 16, or × 20.

STRATIGRAPHIC FIRST APPEARANCES

Cooper (1956, 1976) suggested that the earliest spire-bearing species (still un-named) occurs in the Crown Point Limestone, which has a Conodont Fauna (CF) 6 (*Pygodus anserinus* to *P. serrus*. Sweet and Bergstrom 1976), graptolite Zone 10 (late *Glyptograptus* cf. *G. teretiusculus*. Berry 1976), or an Ashby, pre-Blackriver brachiopod correlation (Cooper 1976, p. 177). In the British succession the Crown Point would probably be of upper Lower Llandeilo age (text-fig. 1). Unfortunately the internal structure in this un-named and undescribed species is unknown, and material is so scarce that the few specimens in question may well be camerellids or smooth rhynchonellids, from which they are difficult to distinguish (see Raymond 1911). Cooper (1956) reported ribbed zygospirids (= *Anazyga*) and smooth spire-bearers (= *Manespira* this paper) from CF7 formations such as the Lebanon of Tennessee and Little Oak of Alabama. Thus by very early Caradoc time (Costonian),
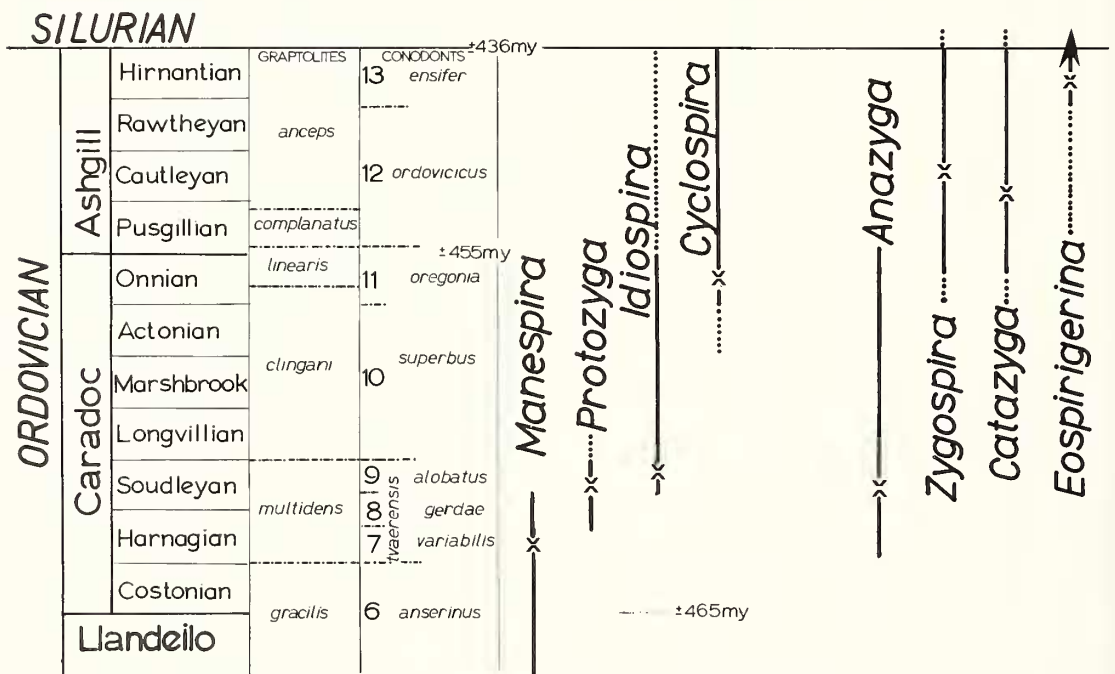
TEXT-FIG. 1. Stratigraphic ranges and first appearances of the Ordovician atrypoids. Smooth atrypoids on the left, ribbed on the right. The 'x' in the lineage marks the occurrence of the type species of the genus. The ranges of conodont and graptolite zones are shown for comparison.

at least two stocks co-existed, both very small shells less than 5 mm wide, one including *Anazyga*, the other *Manespira*. By Blackriver time (Soudleyan, Conodont Fauna 8: Sweet and Bergstrom 1976), in the Napanee Limestone of eastern Ontario and north-eastern New York, the spire-bearers *Protozyga exigua*, *Idiospira panderi*, and *Anazyga* cf. *A. recurvirostra* co-occur in the same stratigraphic horizons though not necessarily at the same localities or in the same bed (text-fig. 1). This strongly suggests that, if North America represents the centre of early spire-bearer evolution (as appears likely at present), first diversification of the spire-bearers occurred by or during CF7 (Harnagian) time.
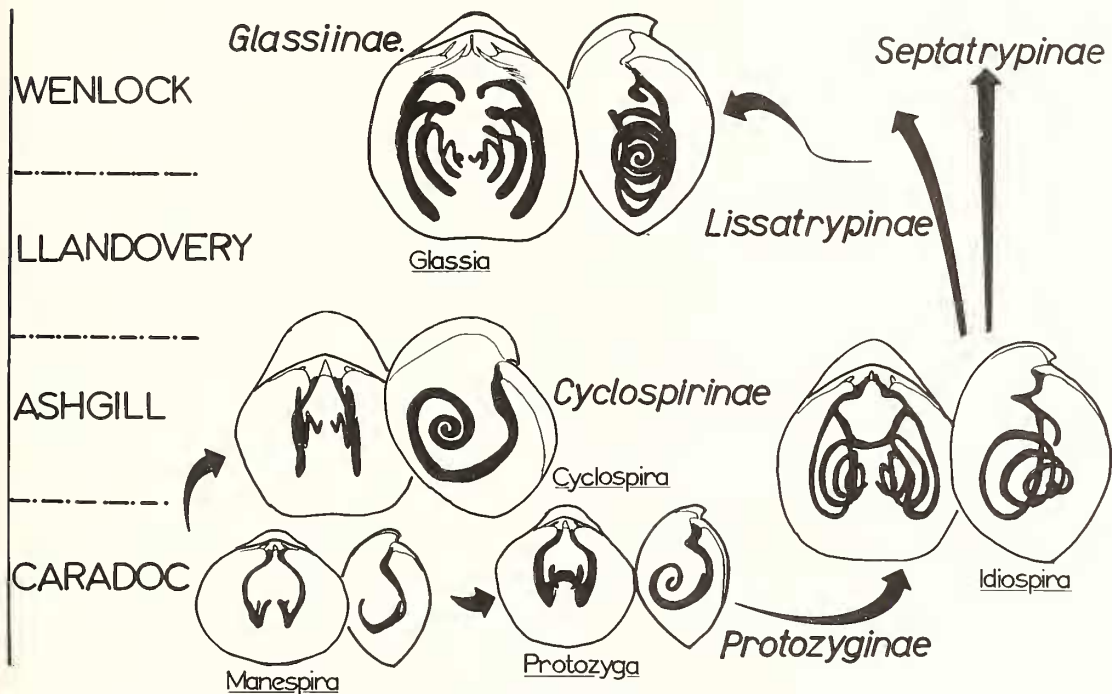
TEXT-FIG. 2. Evolutionary trends in the brachidia of the smooth atrypoid spire-bearers in the Ordovician–Silurian. Note the modifications of the spiralium orientation and jugum with time.

By CF8 time (Harnagian–Soudleyan), *Protozyga* had evolved from *Manespira* by extending the simple whorls, expanding the jugum, and widening the spiralial blade (see text-figs. 2, 5). The ribbed *Anazyga* continued, not giving rise to true *Zygospira* and *Catazyga* until the late Caradoc (Onnian). Lastly, *Idiospira* showed the most rapid evolution: a complex spiralium with many whorls and a jugum which had moved posteriorly as early as CF8 time. *Cyclospira* also appeared in late Caradoc time (CF10, Actonian–Onnian), possibly from *Manespira* by complete loss of a jugum, or even possibly independently by never developing a jugum at all, since it may not be surprising to find *Manespira* without the jugum. Earlier so-called *Cyclospira* reported from 'Wilderness' or Porterfield age rocks by Cooper (1956) have here been referred to *Protozyga* or *Manespira*, since typical bisulcate morphology is more common in Ashgill time. In Ontario and New York *Cyclospira* appears suddenly in the late Trenton (Shermanian, Actonian) and disappears equally quickly above that horizon. At the same time as *Cyclospira* in Ontario there are first appearances of internally more complex genera like *Zygospira* (e.g. *Z. raymondi* Foerste) and *Catazyga* (e.g. *C. filistriata* Sproule). CF10 equivalent sedimentary rocks of the interior of eastern North America therefore

mark a renewed phase of spire-bearer innovation, with at least four co-occurring genera of smooth and ribbed atrypoids.

The last cycle of Ordovician spire-bearer evolution is marked in the Gamachian Ellis Bay Formation of Anticosti (CF13 = Hirnantian, and possibly partly Rawtheyan) with the sudden appearance of abundant *Eospirigerina* and *Hindella*, precursors of the Silurian Atrypidae and Meristellidae respectively. These taxa probably represent immigrants from the north-west USSR or central Asia, moving eastwards across the Baltic and USSR (Jaanusson 1979). Corroboration for this may lie with the discovery of possibly the oldest, late Caradoc, athyroids (*Weibeia* and *Apheathyris*, with laterally directed spiralia), recently described from North China by Fu (1982). *Eospirigerina* makes a first appearance in Eurasia in the *Dicellograptus complanatus* graptolite or low *Amorphognathus ordovicicus* CF12 zone, in rocks of probably early to mid-Ashgill (Pusgillian–Cautleyan) age. This immigration may account for the lack of 'transitional' North American species leading to *Eospirigerina* and *Hindella* in the late Ordovician of eastern North America. Thus, although the subtropical to tropical carbonate shelf environments of North America appear to have been the ancestral 'home' of the atrypoids in Llandeilo to Caradoc time, the more 'advanced' Silurian Atrypidae which replaced them seem to have originated elsewhere.

Finally there are the Silurian first appearances of new stocks of smooth atrypoids. The first of these was the appearance of the Lissatrypinae in late Rhuddanian (A3) time: this group was characterized by generally thicker shells, separated jugal processes and solid teeth without dental cavities. A second development was the introduction in late Llandovery or early Wenlock time of the subfamily Glassiinae, a unique group in which the spiralia were directed towards the shell centre (earlier *Glassia* have been recorded but not confirmed). This spiralium orientation seems to have evolved by neoteny.

Quite independently, the *Spirifer* group, *sensu restricto*, made its first appearance in middle Llandovery (Idwian) time. Three genera appear almost synchronously in China: *Yingwuspirifer*, *Eospirifer*, and *Striispirifer* (Rong and Yang 1978). On Anticosti Island, *Eospirifer* makes its first appearance in the upper 50 m of the Jupiter Fm. of Telychian (C4–5) age. In north-west Europe, the athyroid brachiopod group, the Dayiinae, with very simple juga and spiralia, appeared in Ludlow time.

PHYLOGENY AND ONTOGENY OF THE SPIRALIA

The atrypoid brachiopods are typified by having spiralia that are medially, dorsomedially or dorsally directed. Spiralia are attached to the dorsal shell hinge by means of crura. The athyroids and spiriferoids, on the other hand, had laterally or ventrally directed spiralia, i.e. 'inside-out' opposites of the atrypoid spiralia. *Manespira* n. gen., the oldest spire-bearer known, had a spiralium which consisted of less than one complete whorl coiled in the plane of symmetry, with the tip of the spiralium twisted in a medial direction. The spiralium here is essentially an elongated crus. The jugum may be complete or incomplete (text-figs. 2, 6). Usually the rhynchonellids have been identified as the ancestral group (e.g. Rudwick 1960), by virtue of their earlier appearance in Llanvirn time, shell similarities, hinge, and crura. An alternate ancestral possibility is the Llanvirn or Llandeilo pentamerids, e.g. camerellids, by loss of the cruralium, elongation of the crura and development of the delthyrium. The camerellids possess a smooth shell: in fact, old museum collections sometimes list early atrypoids like *Idiopira* and *Protozyga* under the name *Camerella*, accentuating the morphologic similarity.

Early work on the ontogenetic development of spiralia, within species such as *Anazyga recurvirostra* (Hall) by Beecher and Schuchert (1893), had great influence in suggesting phyletic affinities of the spire and loop-bearing brachiopods. They tried to demonstrate that zygospirid brachidia were initiated as anteriorly fused, bladed crura which gradually diverged but remained connected by development of a jugum between them. The early growth pattern is at least superficially similar to loop construction in the terebratulids. The Beecher–Schuchert model was taken over by Williams and Wright (1961) and Williams and Hurst (1977), who speculated that a 'centronelliform loop'

was developed by the atrypoid *Manespira elongata* (Cooper) from the Bromide Fm. (Caradoc) of Oklahoma. However, the terebratulid loop appears to have been derived entirely independently during the early Devonian since no post-Caradoc *Protozyga* or *Manespira* have ever been described, leaving a time gap of more than 60 million years between these earliest atrypoids and the oldest terebratulids. There is no direct evidence to link the development of the spiralia and jugum in atrypoids with the development of the loop in terebratulids. The jugum as a single, complete structure was abandoned and replaced by separated jugal processes in the Silurian atrypoids, but its retention in all the athyroid and spiriferoids stocks suggests that if the loop developed from the jugum, a possible source of terebratulids lies with smooth athyroids. But, the terebratulids could also have evolved from pentamerids, which lacked a calcified lophophore support. Samtleben (1972), by examining detailed micro-structure of the spiralia and loops using scanning electron microscopy, has convincingly demonstrated that the jugum of spire-bearers is unrelated to the terebratulid loop.

Beecher and Schuchert (1893) were also the first to suggest that there was a fundamental distinction between the atrypoids, 'with spirals between the first descending branches of the lamellae', and the Spiriferidae, Nucleospiridae, and Athyridae, where 'the primary lamellae are between the spirals'. In the atrypoids the crura sweep laterally, changing to the lamellae of the spiralia, with the spiralia coiled towards the centre or dorso-medially between them. In the athyroids and spiriferoids the crura stay close together in the shell middle, changing into spirialial lamellae which are then directed laterally or latero-ventrally. In several early athyroids the spiralia are not connected by solid calcite ribbons to the spiralia, but by interlocking 'hooks'. The Ordovician smooth (and ribbed) atrypoids appear to have had continuous calcite growth from crura to spiralia, though the junction between the two is sharply geniculate (text-figs. 2, 4, 6).

The role of the jugum is not clear in the atrypoids. The oldest spire-bearer, *Manespira*, lacked a complete jugum in its adult stages. In *Protozyga* and *Anazyga*, its descendants, and in other Ordovician atrypoids (except *Eospirigerina*) the jugum was a complete, single piece, either U-shaped or W-shaped. In all atrypoids, the jugum seems to have evolved its morphology independent of the main trends in the evolution of the spiralia. For example, the conversion of a one-piece jugum to two jugal processes occurred in several unrelated lineages. Another factor in jugum evolution is the change with time in disposition of the jugum. Older Ordovician genera show a jugum in an anterior position (e.g. the Protozyginae). Later smooth spire-bearers have a posterior position for the jugum or jugal processes (text-fig. 2). Moreover, the general position shifted as well from a dorsal location to a more ventral location in Silurian taxa (text-fig. 3). It seems possible therefore that the jugal complex played no direct lophophore-supporting role, unlike the terebratulid loop. Instead it may have served to support the mouth parts (its central location in the brachial valve supports this idea), or to have acted as a holdfast for muscles to manipulate or support the spiralia (many jugal processes were provided by spines and these may have served to hold the spiralia in place).

In all the main atrypoid lineages, whether ribbed or smooth stocks, there were parallel trends in the development of the brachidia (jugum and spiralia). These were as follows:

1. Increasing the amounts of internal shell space occupied by the spiralia, and increasing numbers of revolutions of the spiralia. By Silurian and certainly Devonian time (for which shells wider than 60 mm are known), spiralia came to occupy as much as 80 to 90 % of the internal shell cavity.

2. Rotation of the spirialial cones from medial to dorso-medial to nearly dorsal orientation (with the exception of the Cyclospirinae and Glassiinae which adopted a medial orientation). This dorsal orientation allowed the apices of the spirialial cones to grow as large as dorsal valve convexity permitted.

3. Relocation of the jugum from a dorso-anterior position to ventro-posterior position (the Cyclospirinae having no jugum). The position of the jugal complex was usually at or near the apices of the spiralia and this shift may thus have reflected exhalant water canalization.

4. Conversion of a one-piece jugum to separated jugal processes for most atrypoids by Silurian time (with the exception of the Zygospiridae, which were 'living fossils' in the early Silurian, retaining a jugum). This may have avoided breakage of the jugum in higher-energy conditions.

TAXONOMY

The taxonomy of the smooth spire-bearers is far from being settled in a completely satisfactory manner. This is particularly true for the Atrypida, with medially or dorsally directed spiralia, and the Athyrida, with laterally directed spiralia (as defined herein). The nature and direction of the spiralia and the location of the jugal complex and nature of the crura to which these were attached, must have been critical to the filter-feeding process. Ancillary shell morphology, i.e. attachment of the shell with or without a pedicle, shell shape, ribbing, and anterior fold, was also related directly or indirectly to filter-feeding efficiency. These features are thereby of prime taxonomic importance in these groups.

Rzhonsnitskaya (1960) separated the *Atrypa* and *Athyris* groups respectively under a new order Atrypida, and the Athyracea under *incertae ordinis*, and later she suggested that these two groups were monophyletic (Rzhonsnitskaya 1964). Rzhonsnitskaya also assigned the Coelospiracea and Dayiacea to the Atrypida, a practice followed by Boucot *et al.* (1965) and in nearly all modern literature. It can be demonstrated that both the *Coelospira* group (including *Bifida* and *Kayseria*) and the *Dayia* group have spiralia and juga like normal athyroids and should thus be assigned to the Athyrida (Copper 1973).

Another vexing question is the relationship of the true spiriferoids to the atrypoids and athyroids. Boucot *et al.* (1965) and Williams and Hurst (1977) have defended the conventional view, first promoted by Davidson in 1881, that all the spire-bearers are related and hence can be grouped under one order, the Spiriferida. Rzhonsnitskaya (1960), Rudwick (1970) and more recently Wright (1979) have advocated a bipartite or tripartite division into separate orders, the Atrypida and Spiriferida (the former including the Athyrida). Wright (1979) specifically selected the orthid subfamily Platystrophiinae, as the probable ancestral line of the true spiriferids, the transition occurring in late Ashgill or early Llandovery time. The requisite parallel conclusion is, of course, that spiralia developed independently in both the athyrids and true spiriferids. Wright argued this point of view on two grounds: the similar strophic hinge and shell microsculpture. Rong and Yang (1978) have shown that *Yingwuspirifer* appears just before *Eospirifer* in the middle Llandovery. The microsculpture of these two oldest spirifers is very finely striated or micro-costellate, so fine that the shells often appear to be smooth. They apparently lack a micropustulose ornament and coarse plications and wide shelf-like area of *Platystrophia*, though Wright (1979) stated this was present in some *Eospirifer*. It is primarily the later spirifers that begin to resemble *Platystrophia*. The problem of ancestry therefore still seems unresolved, yet I would agree with Wright that the *Eospirifer* group, the oldest spirifers, were probably derived independently from the atrypoids and athyroids.

The definition of the order Atrypida used in this paper specifically excludes the Coelospiracea and Dayiacea. The Athyrida are treated as a distinct order characterized by laterally directed single or double spiralia, which are normally derived from centrally located, anteriorly directed crura, and a simple to highly complex, one-piece jugum enclosed within a non-strophic shell with narrow hinge. Genus level and subfamily level criteria in the Atrypida are considered to be the nature of the shell surface (ribbed, smooth, etc.), convexity, flexure of the anterior commissure, the beak area (foramen, interarea), and hinge structures (teeth, socket plates). Muscle attachment scars yield ambiguous information at present. Muscle scars, vascular canals and gonadal pits are very faint or absent in all early atrypoids.

SYSTEMATIC PALAEONTOLOGY

Order ATRYPIDA Rzhonsnitskaya, 1960 (emend.)

Diagnosis. Smooth or ribbed brachiopods, usually with small interareas and beaks, primarily non-strophic shells, medially to dorsally directed spiralia located between divergent crura and primary lamellae; jugum or jugal processes dorsal to ventral, some lacking jugal complex.

Family LISSATRYPIDAE Twenhofel, 1914

Diagnosis. Smooth atrypoid shells with medially, dorso-medially, or dorsally directed spiralia, jugum or jugal processes or without a jugum.

Subfamilies included. Protozyginae n.subfam., Lissatrypinae Twenhofel, 1914, Glassiinae Schuchert and Levene, 1929, Septatrypinae Kozlowski, 1929, Cyclospirinae Schuchert, 1913.

Names discarded as synonymous. Subfamily Atrypellinae Poulsen, 1943 (= Lissatrypinae), Atrypopsinae Poulsen, 1943 (= Septatrypinae), Aulidospirinae Williams, 1962 (= Cyclospirinae).

Remarks. The late Silurian genus *Australina* Clarke, 1913 from Argentina is not a senior synonym of the North American genus *Lissatrypa* Twenhofel, 1914 (Copper, Hünicken and Benedetto, in preparation), as suggested by Strusz (1982a, b). *Australina* differs externally in its planoconvexity, having a strongly inflated pedicle valve and concave to flattened brachial valve. *Lissatrypa* has a biconvex to weakly dorsibiconvex shell, as well as having distinctive internal pedicle constrictions and cardinalia. An approximate Ordovician–Silurian phylogeny is given in text-figs. 2, 3, 18.
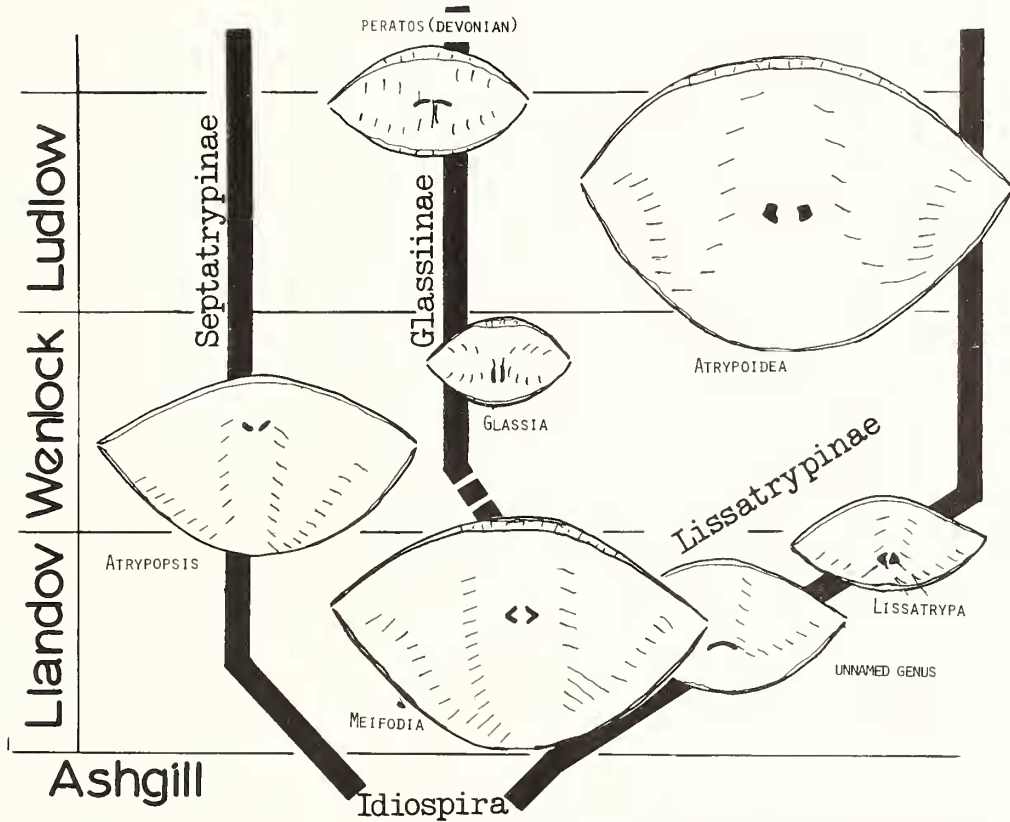
TEXT-FIG. 3. Nature of the jugum and spiralia in the Silurian Lissatrypidae subfamilies. Representative serial sections shown were taken at maximum spiralium size. The ends of the jugal processes, i.e. usually the jugal plates, are superimposed on these serial sections although these normally do not extend to mid-shell. Note that all Silurian smooth atrypoids have separated jugal processes but for one un-named new genus from Anticosti. All specimens to scale of ×2.

Subfamily PROTOZYGINAE n. subfam.

Diagnosis. Small, smooth or anteriorly corrugated, planoconvex to biconvex, sulcate to rectimarginate shell with simple, medially or vertically oriented spiralia normally of two whorls or less, and a simple, whole or partially developed anterior or central-dorsal jugum.

Genera assigned. Protozyga Hall and Clarke, 1893, *Manespira* n. gen.

Range. Llandeilo–Caradoc.

Distribution. North America, north-west Europe, south-east Asia.

Remarks. This subfamily includes the oldest known spire-bearing genera and is distinguished primarily by its brachidial simplicity: a very simple coil or partial spiralial whorl and a partly or fully developed anterior to dorsal jugum. A small, smooth shell (usually less than 5 mm wide), with a straight or sulcate commissure (the opposite of later atrypoids which are usually plicate), and a small, pointed beak with minute foramen characterizes external morphology. The cyclospirinids also have medially directed spiralia with few coils, but they lack a jugum and appear to have a thick ventral valve, stronger dentition, and a relatively long dorsal median septum.

Genus PROTOZYGA Hall and Clarke, 1893

Type species. Atrypa exigua Hall, 1847, p. 141, pl. 33, fig. 6a–d. CF8: Caradoc, late Harnagian–early Soudleyan.

Range. Blackriveran–Trentonian (early–middle Caradoc), ?Ashgill.

*Distribution.* North America, Europe, south-east Asia.

Diagnosis. Normally smooth, planoconvex-ventribiconvex, sulcate shells with small incurved beak, minute pedicle opening and deltidial plates, medially pointed or planispiral spiralia of one or more dorso-ventrally oriented coils, giving rise anteriorly to simple, broad jugum directed posteriorly. Thin shells with dental cavities and simple hinge structure, very weakly defined muscle scars, weak dorsal septum.

Remarks. Since the whorls are nearly planispiral, it is difficult to determine in which direction a single coil may be oriented, except that in the type, *P. exigua* (text-fig. 4), the terminal part of the whorls is located towards the centre in relation to the ascending lamella. This means that for the type species the spiralia are medially directed. It is not impossible, however, that other related species may be planispiral, the difference in direction being only a matter of a millimeter. This suggests that the Protozyginae may also have been potential ancestors of the Athyrida, which are typified by laterally directed spiralia. The oldest athyroids appear, as presently known, in late Caradoc time (Fu 1982). There is a substantial time gap between the oldest Athyrida and youngest protozyginids in the stratigraphic sections of North America and western Europe, suggesting important easterly migrations in Ashgill time.

 Protozyga differs from *Manespira* in a bigger shell, in usually having a smooth, even shell surface (though this may be present in some *Manespira*), and in lacking corrugations on the commissure. *Protozyga* has a more complex spiralium of one or more revolutions (maximum observed was two), and a complete one-piece jugum.

 Most of the species of *Protozyga* have been described by Cooper (1956) from Caradoc rocks of the eastern US (Oklahoma to Virginia). For these species the spiralia are unfigured except for one. If Cooper's species are distinctive enough to be recognized, it implies great variability in the group, all species of which fall within two conodont zones. Four of Cooper's species of *Cyclospira* have been tentatively assigned to *Protozyga* until their spiralia can be verified.

Species assigned. ?Protozyga haydeni Reed, 1936, p. 51, pl. 4, fig. 12, 'Hill behind Taunggyi', southern Shan states, Burma; Caradoc. A single cast of a brachial valve is the only specimen available. Affinities doubtful.

inward spiralium
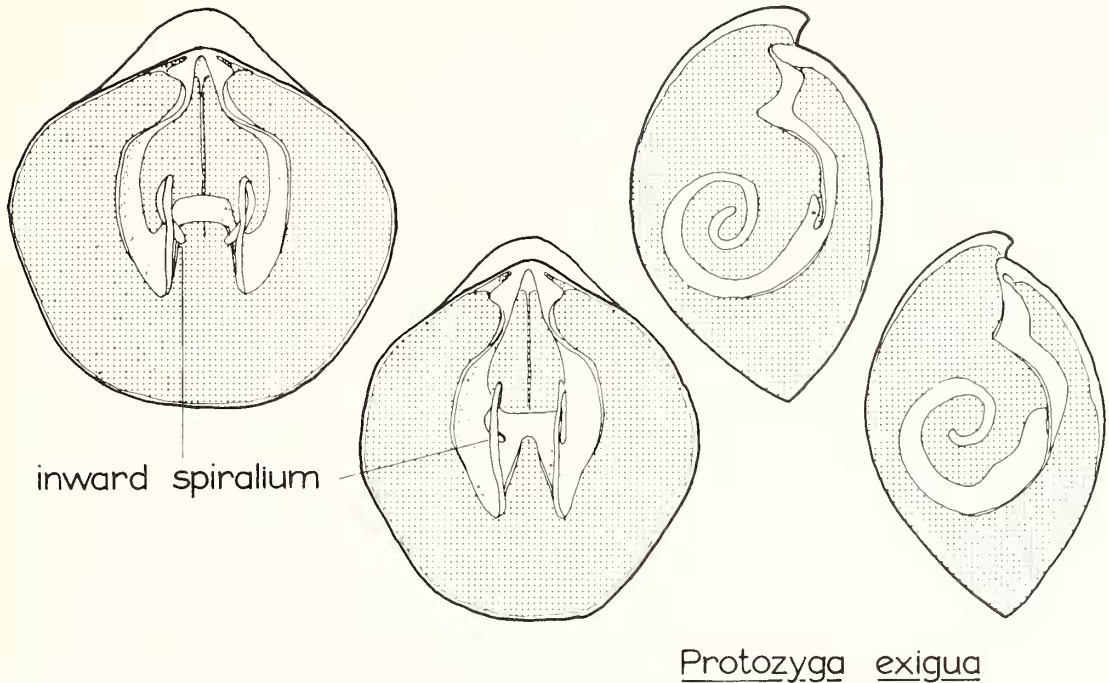
Protozyga exigua

TEXT-FIG. 4. Brachidia of two specimens of *Protozyga exigua* (Hall, 1847) based on text-fig. 5. Note the broad ascending (primary) lamellae, centro-dorsal jugum, and simple spiralium (lateral view shows only one spiralium). Scale × 8.

?*Protozyga jingheensis* Fu, 1982, p. 160, pl. 42, fig. 11*a–d.* Dongzhuang, Liquan, Shaanxi, China; Jinghe Fm., Caradoc. This species has a fold in the dorsal sulcus. Internal structure unknown.

Protozyga loeblichi Cooper, 1956, pp. 679–680, pl. 140c, figs. 17–21. Bromide Fm., Pooleville Mbr (CF 7), Oklahoma; Caradoc. Species with one or two plications on the commissure. Brachidia unknown.

Protozyga microscopica Cooper, 1956, p. 681, pl. 141D, figs. 22–24; pl. 141F, figs. 33–37. Lincolnshire Fm., Hogskin Mbr, Tennessee; Caradoc. Brachidia unknown.

Protozyga nasuta Cooper, 1956, pp. 681–682, pl. 141G, figs. 38–41. Whistle Creek Fm., Virginia; Caradoc. According to Cooper, below the Lincolnshire Fm. Brachidia unknown.

Cyclospira parva Cooper, 1956, p. 694, pl. 142K, figs. 49–53. Bromide Fm., Pooleville Mbr, Oklahoma; Caradoc. Cooper reported that the spiralium extended well beyond the shell centre, but the absence of a jugum, as typical of *Cyclospira*, was not mentioned.

Cyclospira preciosa Cooper, 1956, pp. 694–695, pl. 141E, figs. 25–32. Edinburgh Fm., Virginia; Caradoc. Cooper mentions 'descending processes of spire reaching nearly to front margin', suggesting *Protozyga*.

Cyclospira quadrata Cooper, 1956, pp. 695–696, pl. 141A, figs. 1–12; pl. 143B, figs. 7–11. Edinburgh Fm., Virginia; Caradoc. Externally similar to *Protozyga exigua*, but brachidia unknown.

Protozyga rotunda Cooper, 1956, pp. 683–685, pl. 140B, figs. 10–16; pl. 140M, figs. 48–52; pl. 140I, figs. 53–58. Wardell Fm., Tennessee; Caradoc. It has one or two obscure plications on the flanks and may be conspecific with *P. loeblichi*. Brachidia with 'a long descending branch . . . jugum complete' (Cooper, 1956, p. 684). Williams (1962) stated that he identified this species in Llandeilo rocks of Girvan, UK.

Protozyga rotundiformis Cooper, 1956, p. 685, pl. 140J, figs. 59–62. Lincolnshire Fm., Tennessee; Caradoc. Has one or two plications; brachidia unknown. This species may belong to *Manespira* and/or be a variant of *P. microscopica*.

Cyclospira sulcata Cooper, 1956, p. 696, pl. 142m, figs. 60–69. Sevier Fm., Tennessee; Caradoc. The smooth shell suggests an elongate *P. exigua*. Brachidia unknown.

Protozyga tianzuensis Fu, 1982, p. 160, pl. 42, fig. 10*a–d*. Hengliang Mtn, Tianzhu, Gansu; Goulang Fm., Caradoc. Brachidia unknown.

Species deleted. Protozyga gastrodes Temple, 1968, referred to *Cyclospira*.

Protozyga musculosa Lockley, 1980, p. 218, figs. 70–76. Bed TB19, Nod Glas, Nant Tan y Blwch, Wales; Caradoc. Illustrations indicate dental plates nearly half the shell length. This is not known from any atrypoid. Affinities questionable. No spiralia described.

Protozyga perplexa Williams, 1962, referred to *Cyclospira*.

Protozyga carrickensis Reed, 1917, referred to *Idiospira*.

Protozyga profunda Cooper, 1956, p. 683, pl. 143a, figs. 1–6. Trenton Fm., St Francis de la Salle Quarry, Montreal. Examination of topotype material sent by Dr. G. A. Cooper shows that this species is finely ribbed and assignable to *Anazyga*, a zygospirid.

?*Protozyga obsoleta* Foerste, 1914, p. 133, pl. 2, fig. 10*a–b*, 'lower part of the Millersburg Member, Cynthiana Fm.', CF10, Ashgill. Internal structures were not examined by Foerste, who, however, noted that the shell had a shape and ribs similar to *Zygospira*, where it should probably be assigned.

Protozyga exigua Hall, 1847

Pl. 73, figs. 1–5; text-figs 4, 5

1847   *Atrypa exigua* Hall, p. 141, pl. 33, fig. 6*a–d*.
1893   *Protozyga exigua* Hall; Hall and Clarke, p. 149, figs. 137–138.
1956   *Protozyga exigua* Hall; Cooper, pp. 678–679, pl. 119d, figs. 9–14; pl. 140f, figs. 38–42; pl. 141g, figs. 29–33.

Type locality. 'Lowville and near Martinsburg, Lewis County', New York (Hall 1847). The exact locality is unknown, and is not indicated with the type materials (Cooper 1956, pp. 675–6 and personal examination). No new localities at which this species is abundant could be found in New York.

Type horizon. 'In the central part of the Trenton Limestone' (Hall 1847, p. 141). Titus (pers. comm.) says that Hall was almost certainly mistaken here, and that he and colleagues have found it only in the lower Trenton, specifically most abundantly in the Napanee Limestone (source of the serially sectioned specimen: text-figs. 4–5), but as low as the underlying Selby Lst. Both of these limestones belong in the CF8 zone.

Type specimens. A lectotype, AMNH 714–1a, was selected by Cooper (1956, pl. 142g, figs. 29–33), from five syntypes in the Hall collection.

EXPLANATION OF PLATE 73

Figs. 1–5. *Protozyga exigua* (Hall, 1847). Lectotype AMNH714a, imperfect specimen with faintly corrugated lateral commissure. 'Lowville, New York'; probably Napanee Limestone, CF8, Soudleyan, Caradoc, × 5.

Figs. 6–20. *Manespira nicolleti* (Winchell and Schuchert, 1892). East of Chatfield, Minnesota; McGregor Mbr, Platteville Fm., CF7 or CF8, Harnagian–Soudleyan, Caradoc, × 5. Relatively variably corrugated species, one of the youngest survivors in the genus. 6–10, Neotype GS59146, a large adult shell, nearly smooth in early growth stages (small carbonate fragment adhering to ventral umbo); 11–15, medium-sized shell GS59147; 16–20, small shell GS59148.

Figs. 21–35. *Idiospira panderi* (Billings, 1859). All material from 'Paquette Rapids' type locality, east Ontario (Ottawa Valley); high Napanee or Kings Falls Limestone, late CF8 or early CF9, Soudleyan, Caradoc, × 3. Specimens are partly or wholly silicified. 21–25, lectotype GS1149c, partly damaged specimen, one of six syntypes from Billings collection. 26–30, paralectotype GS1149b, a more elongate variety showing strong 'beeckite' silicification. 31–35, hypotype ROM23918a, whole specimen, nearly identical to the Billings lectotype to show the distal development of the shell corrugation and the uniplicate fold.

PLATE 73

COPPER, Ordovician atrypoids
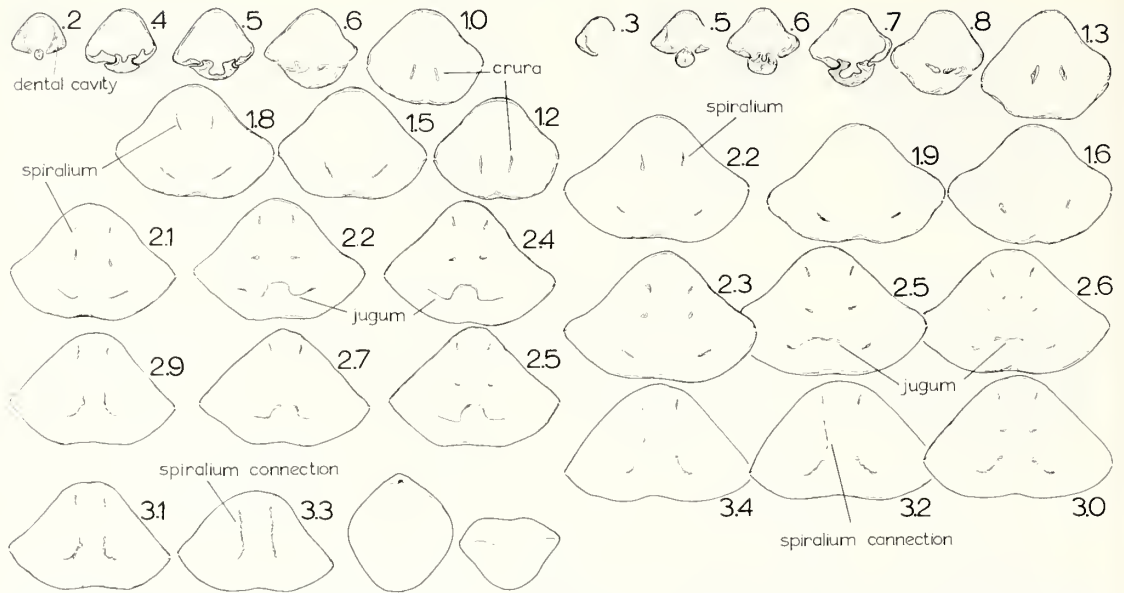
TEXT-FIG. 5. Serial sections of two specimens of *Protozyga exigua* (Hall, 1847). Napanee Limestone, near Napanee, Ontario, NTS 31C/7W 44600:02930; Caradoc, Harnagian–Soudleyan. Note that spiralium connection occurs near the anterior commissure. Scale × 4.

Diagnosis. Small, smooth, with faint trace of ribs at commissure, ventribiconvex to planoconvex, 3 to 5 mm wide, about as wide as long, subquadrate to somewhat pentagonal shell with narrow apical angle (100°–110°) and sulcate margin, anteriorly rounded. Beak anacline to hypercline.

Proportionally large, wide dental cavities and subhorizontally directed teeth, no pedicle layers in umbonal cavity. Socket plates thin, but long, crural bases and inner socket ridges relatively prominent, bulbous; crura directed as dorso-ventral strong blades, broadening and curving laterally to form prominent ascending lamellae and terminating in a narrowing spiral band of one to two revolutions. Jugum W-shaped with broad central-ventral arch; jugum may be curved posteriorly (text-fig. 5). Weak dorsal septum divides adductors.

Remarks. There is no fresh information on the nature of the spiralia and jugum in other species of *Protozyga*. The internal details of *Protozyga elongata* Cooper, 1956, illustrated by Williams and Wright (1961, text-fig. 4) indicate that the species *elongata* should be referred to *Manespira* on the basis of its primitive brachidia. Hall and Clarke (1893, p. 149) illustrated the primitive nature of the brachidia of *Protozyga* for the first time, and their illustration is essentially correct except in showing a very narrow, instead of broad and wide ascending lamella and a thin anterior jugum. This may be infraspecific variation. Weller (1903, pl. 10, figs. 27–30) illustrated a *Protozyga* from New Jersey which is similar to *P. exigua* but more elongated and with a narrower hinge angle.

Titus and Cameron (1976) indicate that *Protozyga exigua* occurs in the *Liospira* and *Triplesia* communities that occupied a carbonate shoal to lagoonal marine facies. This was a deeper, quieter, high diversity environment ranging to shallower, higher energy zones. *Protozyga* is apparently nowhere abundant in New York or Ontario, representing only a very minor fraction of the community. The typical lithology is a medium to thickly bedded micrite with shale partings, minor broken shell layers and occasional *Solenopora* algal balls.

Materials. Protozyga exigua is not uncommon in the Napanee Limestone near Napanee. In New York it occurs near Lowville, Sugar River, and Port Leyden (Cooper 1956), but is rare. It characterizes the upper

Rocklandian Napanee Limestone (CF8, approximately Harnagian–Soudleyan), and is associated with two other spire-bearers, *Anazyga* and *Idiospira*. Sectioned comparative material came from a Highway 401 roadcut about 4 km north-east of Napanee (NTS 31C/7W 44600:02930), marked on the map as Gull River Fm. by Liberty (1971), but belonging to the Napanee Limestone, which is assigned by Liberty to the Bobcaygeon Fm. *Protozyga* has not been found in the northern Michigan Basin (Manitoulin) nor in Quebec.

MANESPIRA n. gen.

Name. Mane, Latin, dawn or morning, and *spira*, spire or coil.

Type species. Hallina nicolleti Winchell and Schuchert 1892, p. 293, and 1893, p. 474, pl. 34, figs. 50–62. Platteville Fm., McGregor Mbr (CF8: Sweet and Bergstrom 1976); Minnesota.

Range. Late Llandeilo–middle Caradoc (middle Soudleyan). Cooper (1956, 1976) reports the earliest possible spire-bearers from the Ashby stage (about early CF6 of Sweet and Bergstrom, 1976). This was based on two specimens, one from the Crown Point Fm. of New York and one from the Row Park Fm. of Maryland, neither of which have been figured or described or examined for spirialial configuration. This material may belong to *Manespira*. No further specimens have yet been discovered (pers. comm. G. A. Cooper, D. Fisher, H. J. Hofmann, T. M. Clarke, C. W. Stearn). Williams (1962) identified *Protozyga rotunda* from the Confinis Flags at Girvan, which are of Llandeilo age. Cooper described three species of *Protozyga* (here assigned to *Manespira*) from the Mountain Lake Mbr of the Bromide Fm., slightly younger than the Crown Point Fm. and probably of upper CF6 or lower CF7 age. One of the youngest *Manespira* is the type species, from CF8 equivalents in Minnesota, where it is very abundant.

Diagnosis. Small, ventribiconvex to biconvex, sometimes weakly ventrocarinate shells with smooth umbonal regions, smooth or corrugated anterior and lateral commissure, weakly sulcate, small anacline to hypercline beak. Internally thin shelled, small dental cavities, minute deltidial plates, delicate medially directed teeth; thin socket plates, laterally pointed crura curving dorsally into ascending lamellae, in turn giving rise anteriorly to a dorsal complete or incomplete jugum, and ventrally into a revolution of one whorl or less. Median dorsal septum absent or faint.

Remarks. Manespira is distinguished from *Protozyga* by its possession of a primitive brachidial apparatus with a spiralium of less than one complete whorl, a dorso-anterior complete or incomplete jugum and a shell normally typified by corrugations, even leading to the appearance of a small fold in the dorsal sulcus (text-fig. 6). The calcified brachidial apparatus occupies only a small part of shell volume. Contemporaneous *Anazyga* are distinguished by their finely ribbed shells and spiralia with several revolutions, and probably evolved from *Manespira* in early Caradoc time. Suppression of jugal development and hinge modification could also have led to the evolution of *Cyclospira* from *Manespira* in late Caradoc time.

  Manespira is similar to the Ashgill genus *Zygospira (Sulcatospira)* Xu, 1979, from the Qinghai Plateau, China, in having relatively coarse corrugations or costae, but the latter is closely related to, if not a junior synonym of *Zygospira (Zygospira)*, since it has more complex dorso-medial spiralia with four or more revolutions. Xu distinguished *Sulcatospira* from *Zygospira* by its possession of a strong dorsal fold but commonly *Zygospira* specimens also have a dorsal sulcus interrupted in the centre by a strong costa or corrugation which leads to the production of a central, dorsal 'fold' like that of *Sulcatospira*.

  A second, more enigmatic Ashgill Chinese genus is *Manosia* Zeng, 1983, from the Yangtze Gorge area. This is a partly smooth, partly coarsely ribbed or corrugated shell somewhat similar to *Manespira* in form except in showing many costae and larger shell size: Zeng compared it to triplesioids with a question mark, but the shell may be an atrypoid. Internal structure is unknown.

Species assigned. Protozyga costata Cooper, 1956, pp. 676–677, pl. 142A, figs. 1–5. Bromide Fm., Mountain Lake Mbr, Oklahoma; Caradoc. Brachidia undescribed. In view of the considerable rib and shape variation seen in *Manespira nicolleti*, it seems possible that *M. costata* and *M. elongata* (below) are conspecific. Sweet and Bergstrom (1976) indicate that the CF6 and CF7 boundary is located within the Mountain Lake Mbr (i.e. approx. late Costonian).

?*Cyclospira diversa* Reed, 1917, p. 150, pl. 24, figs. 37–43. Basal Ardwell Mudstones (mid-Caradoc), Ardmillan Braes, Girvan, Strathclyde. Brachidia unknown. Williams (1962, pl. 25, figs. 19, 25, 26) illustrated a damaged specimen with a strong sulcus. This is a doubtful *Manespira*.

Protozyga elongata Cooper, 1956, pp. 677–678, pl. 140E, figs. 27–37; pl. 143I, figs. 41–46. Mountain Lake Mbr, *Doleroides* Zone, Oklahoma. Williams and Wright (1961, p. 158) illustrated a growth series of the brachidia for this species, showing a simple jugum and partial first whorl which indicate assignment to *Manespira*. Late CF6 or early CF7, late Chazyan–early Blackriveran; Costonian.

Protozyga magnicostata Cooper, 1956, p. 680, pl. 140A, figs. 1–9. Bromide Fm., Mountain Lake Mbr; Caradoc. Brachidia unknown. Possibly a deeply ribbed variant of *M. costata*.

Protozyga tumida Cooper, 1956, p. 687, pl. 140G, figs. 43–47; pl. 141I, figs. 46–50. Effna Fm., Virginia. The four to five corrugations on the flank indicate *Manespira*; brachidia unknown. Probably CF6, late Llandeilo or earliest Caradoc.

Protozyga uniplicata Cooper, 1956, pp. 687–688, pl. 140D, figs. 22–26; pl. 141H, figs. 42–45; pl. 141K, figs. 58–62. Benbolt Fm., Virginia; CF7, Caradoc. Brachidia unknown.

No other species have apparently been described. Raymond (1911) identified '*Zygospira acutirostris*' from the Crown Point Fm. in the Lake Champlain area of New York, but Cooper (1956) pointed out that this is assignable to the rhynchonellid *Sphenotreta*. There remains the question of whether *Camerella longirostris* and *C. varians* Billings (1859) from Llandeilo or possibly Llanvirn rocks of the Mingan Islands, Quebec, are early atrypoids. Cooper (1956) assigned the former species to the triplesiid *Onychoplecia* and the latter to *Camerella*. Examination of Twenhofel's Mingan brachiopod collections do not show evidence of spire-bearing.

Manespira nicolleti (Winchell and Schuchert, 1892)

Pl. 73, figs. 6–19; text-figs. 6 and 7; Pl. 75, figs. 3–6

1892   *Hallina nicolleti* Winchell and Schuchert, p. 293 (no figs., publication date cited as 1 April, 1892).
1892   *Zygospira aquila* Sardeson, p. 335, pl. 4, figs. 15–18 (publication date 9 April 1892).
1893   *Hallina nicolleti* Winchell and Schuchert, p. 474, pl. 34, figs. 59–62 (it should be noted that the publication date is shown as 1895 but a published letter at the beginning of vol. 3 states that the first copy of the volume was tendered in December 1891. Nevertheless, Hall and Clarke (1893) cite the publication date as 1893 and this is used here.
1893   *Zygospira nicolleti* Winchell and Schuchert; Beecher and Schuchert, pl. 10, fig. 23 (illustrates brachidia only).
1956   *Protozyga nicolleti* Winchell and Schuchert; Cooper, pp. 682–683, pl. 141J, figs. 51–57.
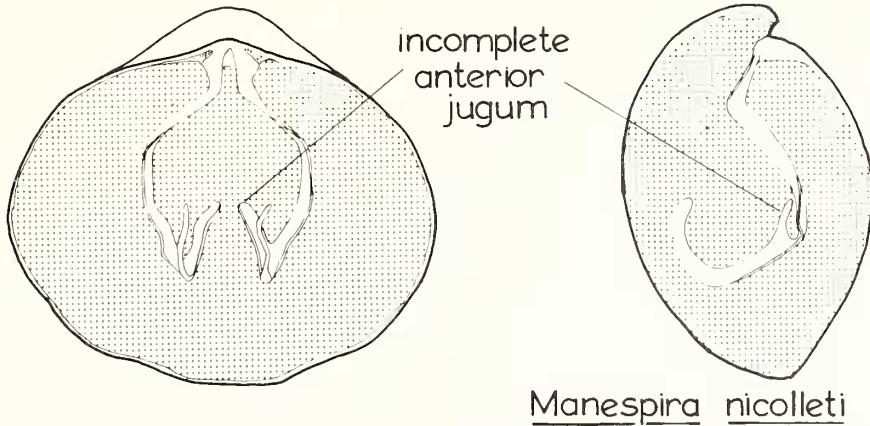1977   *Protozyga nicolleti* Winchell and Schuchert; Bretsky, Bretsky and Schaefer, fig. 9G, p. 124.

Types. The location of the type material is unknown and presumed lost. A neotype is selected herewith: GS59046, with paraneotypes GS59047, 59048, 59068.

Type locality and horizon. '. . . abundant in the upper third of the Trenton limestone at Minneapolis, Rochester and Fountain, Minnesota and Decorah, Iowa' (Winchell and Schuchert 1893, p. 474). The caption to pl. 34, fig. 64 reads 'Fountain, Minnesota' which is the nominal type locality. Cooper (1956) identified the type horizon as the McGregor Mbr of the Platteville Fm., which has a CF8 correlation according to Sweet and Bergström (1976), but may be somewhat lower, i.e. CF7 or early Blackriveran. Bretsky *et al.* (1977) showed that this species is widespread in the lower part of the McGregor Mbr only (the Mifflin Unit) and is extremely abundant, forming up to 13 % of the community. The species was found very abundantly (500 + specimens) at a north side roadcut about 4 km due east of Chatfield along Hwy. 74, Minnesota, some 3 m above a basal sandstone unit. This may be designated a *locus typicus restrictus*.

Associated lithology and fauna. *M. nicolleti* is abundant on micrite bedding-plane surfaces in concentrations of more than 200 per 100 cm². Many were found attached to each other (small to larger shells), but the lime muds may also have formed incipient hardgrounds to which shells were fixed. Bretsky, Bretsky and Schaefer (1977) indicated 'episodically agitated . . . and shallower waters'.

Description. Relatively small shell, 4 to 5 mm wide (rarely 6 mm), about as wide as long, ventribiconvex, with rounded outline and hinge angle of 100–110°. Beak small, anacline, foramen apical (deltidial plates minute, not visible externally), anterior commissure sulcate with raised centre producing a distinct dorsal fold and ventral sulcus; two to four corrugations on lateral commissure, with shell smooth, rectimarginate or weakly

TEXT-FIG. 6. Brachidia of *Manespira nicolleti* (Winchell and Schuchert, 1892), based on text-fig. 7. Note the incomplete jugum and delicate half-whorl of the spiralium. Scale × 10.
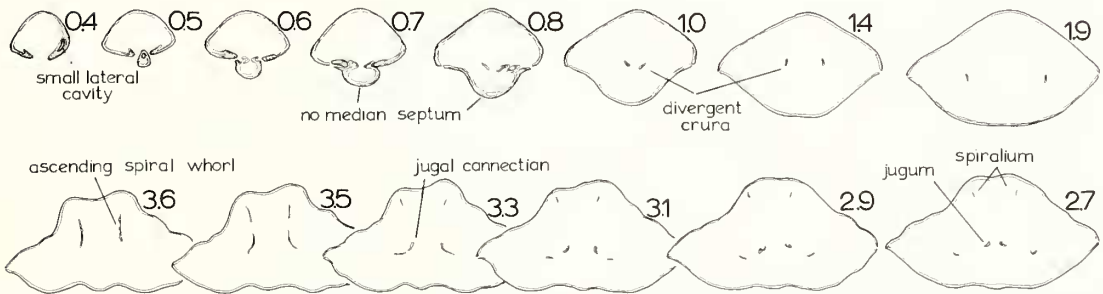
TEXT-FIG. 7. Serial sections of *Manespira nicolleti* (Winchell and Schuchert, 1892). Mifflin Horizon, McGregor Mbr, Platteville Fm., east of Chatfield, Minnesota; Caradoc, Harnagian. GS79443. Scale × 5.

sulcate in early growth stages. Interior of pedicle valve lacking pedicle deposits, large dental cavities and centrally pointed teeth. Crura divergent, ventro-anteriorly directed, curving dorsally to result in ascending lamella; dorsal jugum complete or incomplete, very thin, delicate spiralial half revolution in largest shells (text-figs. 6, 7).

Remarks. Sardeson (1892, pl. 4, fig. 18) showed a one-piece jugum resembling a terebratulid loop. Winchell and Schuchert (1893) illustrated specimens showing as many as seven lateral corrugations on the shell, and, internally, a complete loop-like jugum but no spiralial coil. This feature was not seen in specimens sectioned.

M. *nicolleti* occurs in nest-like concentrations of hundreds of shells, about 60 % of which appear to be tilted at an angle, brachial valve down, shell umbo pointing into the substrate, suggesting life positions. Thus the anterior commissure pointed upwards.

Subfamily SEPTATRYPINAE Kozlowski, 1929

Diagnosis. Smooth or corrugated, plicate, smooth, thin-shelled atrypoids with multi-coiled, dorsally directed spiralia, a posterior jugum or jugal processes, large dental cavities, usually dental plates, thin hinge plates.

Remarks. In this group, the Ordovician genus *Idiospira* is the only genus known with a dorsally located, one-piece jugum (possibly it deserves separate subfamily status). All others, as far as those for which internal structures have been studied, have jugal processes. Internal structure of the problematic late Ordovician genus *Manosia* Zeng 1983 is unknown.

Genus IDIOSPIRA Cooper, 1956

Type species. *Camerella panderi* Billings 1859, p. 302 (illustr. Billings, 1863, p. 143, fig. 78*a–b*), Rockland Fm., Paquette Rapids, Alumette Island, Ontario; Middle Caradoc, Blackriveran, CF8.

Range. Middle Caradoc–Ashgill. Nikiforova and Modzalevskaya (1968) assigned two early Llandoverian Siberian species, *Protozeuga khetaensis* Nikiforova 1942 and *Glassia mogoktaensis* Nikiforova 1961 to *Idiospira*. Specimens of these two species were sectioned, but are not *Idiospira* (the latter remains provisionally assigned to *Glassia*). In Ontario and New York *Idiospira* have a restricted range from the middle Cloche Island Fm. (Bobcaygeon Fm.) to Cobourg Fm., or, Napanee through Denley Limestones, and are absent in Ashgill rocks.

Distribution. North America, Europe, Siberia, China.

Diagnosis. Small, ovoid, biconvex-dorsibiconvex, smooth atrypoids usually with corrugated anterior commissure. Beaks anacline to nearly hypercline, interarea small, apical to expanded foramen, small deltidial plates. Internally with large dental cavities, thin dental plates, horizontal hinge plates, weak septum, crura latero-ventral and geniculated sharply at jugal connection, jugum simple, straight or weakly arched, dorsal in position. Spiralia up to six whorls, directed dorso-medially at about 40–50° to commissural plane.

Remarks. *Idiospira* are distinguished externally from *Protozyga* and *Cyclospira* by their biconvexity, anterior corrugations and dorsal fold. Internally these genera differ radically in their spiralia and jugum.

Idiospira, and a still undescribed genus of smooth atrypid from Anticosti Island related to *Meifodia*, are the only smooth spire-bearers known to have a dorsally located jugum. This appears to be a 'primitive' feature in that later taxa have ventral jugal processes (text-fig. 3). *Idiospira* is 'advanced' in the sense of having spiralia with numerous coils directed dorsally ('primitive' smooth spire-bearers have medially directed spiralia with very few coils). *Idiospira* appears to have replaced *Protozyga* in the late Caradoc or early Ashgill and in turn it was dominated in Ashgill time by ribbed atrypoids such as *Zygospira*, *Catazyga* and *Eospirigerina*. Possibly as many as seventeen described species may be assigned to *Idiospira*, but most species have poorly known or unknown brachidia and require verification.

Species assigned. ?*Protozeuga anticostiana* Twenhofel, 1914, pp. 29–31, pl. 1, figs. 8–10. 'Macasty Bay, zone 4, of English Head Formation' (= Vaureal Fm.), Anticosti Island, Quebec; Ashgill.

?*Camarella* (*sic*) *bernensis* Sardeson, 1892, p. 328, pl. 4, figs. 4–6. 'From the *Camarella* bed at Berne . . . Minn(esota)', Decorah Fm.; Trentonian, late Caradoc. Identified as *Parastrophina* by Cooper (1956), but internals unknown.

?*Hyattidina charletona* Twenhofel, 1914, pp. 34–35, pl. 1, figs. 6–7. 'Charleton Point, zone 3 of Charleton Formation' (= Vaureal Fm.), Anticosti Island; early Ashgill.

?*Atrypa circulus* Hall, 1847, pp. 142–143, pl. 33, fig. 7*a–c*. 'Compact black limestone . . . at Middleville', New York; Trentonian, Caradoc.

?*Rhynchonella cuneatella* Davidson, 1883, p. 200, pl. 10, fig. 11. Balclatchie Conglomerate, Balclatchie, Girvan, UK; early Caradoc. Brachidia unknown; assigned by Cocks (1978).

?*Idiospira gansuensis* Fu, 1982, p. 160, pl. 42, fig. 9*a–c*. Wangyao Valley, Tianzhu, Gansu; Shantai Fm., Llandoverian. Brachidia unknown.

?*Camerella inornata* Weller, 1903, pp. 157–158, pl. 10, figs. 8–10. Jacksonburg Fm., 'Locality 192A', Hainesburg, New Jersey; Trentonian, late Caradoc. A relatively large species, brachidia unknown; assigned by Cooper (1956).

Idiospira lata Su, 1977, p. 301, p. 115, fig. 17. Lower reaches of the Guangniao He [river], Nenjiang County, Heilongjian Province, north-east China; Guangniaohe Fm.; Caradoc. Brachidia unknown.

Cyclospira longa Cooper, 1956, pp. 693–694, pl. 142ɪ, figs. 39–43. Rysedorf Conglomerate, New York; late Caradoc, but possibly reworked specimens. Biconvexity and lack of dorsal sulcus suggest *Idiospira*; brachidia unknown.

?*Zygospira maynei* Roy, 1941, p. 103 = 103, fig. 69. 'Sillimans Fossil Mount, Frobisher Bay . . . Richmond', N. Canada; Caradoc. Brachidia unknown.

Idiospira minor Fu, 1982, p. 161, pl. 42, fig. 6*a–b*. Dongzhang, Liquan, Shaanxi; Beiguoshan Fm., Upper Ordovician (Ashgill). Brachidia unknown.

?*Hyattidina plicata* Mitchell, 1977, p. 127, pl. 17, figs. 29–32. Bardahessiagh Fm., Pomeroy, County Tyrone, Ireland; late Caradoc. Brachidia unknown.

?*Glassia romingeri* Hall and Clarke, 1894, p. 153, pl. 83, figs. 32–35. 'in a drifted boulder of Trenton Limestone near Ann Arbor, Michigan'. The specimen illustrated shows a biconvex, bisulcate shell and medially directed spiralia, unlike other *Idiospira* known. No similar specimens known from probable Caradocian source beds in the northern Michigan basin. Brachidia unknown.

?*Hyattidina sulcata* Williams, 1962, p. 254, pl. 25, figs. 47, 53, 58–60. Kiln Mudstones, Craighead, Girvan; late Caradoc. Brachidia unknown.

Idiospira taoqupoensis Fu, 1982, p. 161, pl. 42, figs. 7–8. Taoqupo, Yao, Shaanxi; Upper Beiguoshan Fm., Ashgill. Brachidia unknown.

Rhynchonella thomsoni Davidson, 1869, p. 186, pl. 24, fig. 18. Craighead Limestone, Craighead Quarry, Girvan; late Caradoc. Brachidia unknown.

Idiospira warthini Cooper, 1956, pp. 692–693, pl. 140ᴋ, figs. 63–72; pl. 195ɢ, figs. 38–41. Wappinger Fm., near Poughkeepsie, New York; Trentonian, late Caradoc, CF10. Brachidia unknown.

?*Idiostrophia* sp. 1 Cooper, 1956, p. 590, pl. 113ᴀ, figs. 1–5. Boulder in Mystic Conglomerate, Range 6, Lot 20, Stanbridge Township, Quebec; late Caradoc or early Ashgill (but reworked, and possibly older). Brachidia unknown.

Idiospira panderi (Billings, 1859)

Pl. 73, figs. 21–35; Pl. 74, figs. 1–5; text-figs. 8, 9

1859 *Camerella panderi* Billings, p. 302 (no figs.).
1863 *Camerella panderi* Billings; Billings, p. 143, fig. 78*a*, *b* (no description).
1893 *Camerella panderi* Billings; Hall and Clarke, p. 220, pl. 62, figs. 19–23.
1932 *Camerella panderi* Billings; Wilson p. 139, pl. 2, fig. 4 (Figs. 1–3, 5 show the septalium-cruralium of *Camerella volborthi*, type species of *Camerella*, which co-occurs with *Idiospira* and may be confused with it).
1946 *Camerella panderi* Billings; Wilson, pp. 118–119, pl. 11, fig. 2.
1956 *Idiospira panderi* (Billings); Cooper, pp. 691–692, pl. 108ғ, figs. 26–32.

Type locality. 'Pauquette's Rapids' [*sic*] (Billings 1859, p. 302) and in Billings (1863, p. 176), 'the best specimens, however, are obtained in the bed of the river'. In an attempt to collect new topotypes, no shells were found on the east side of the Alumette outlier, nor were any fossiliferous outcrops observed on the west side of the Westmeath peninsula facing Paquette Rapids (NTS Fort Coulonge 31F/15W, 49–50: 82).

Type horizon. 'Black River limestone' (Billings 1859, p. 302). Wilson (1946) identified the syntypes as coming from 'Leray-Rockland' beds, equivalent to the Kings Falls Limestone in New York, at the CF8 to 9 transition (Sweet and Bergstrom 1976), or in the Napanee Limestone (CF8). Titus and Cameron (1976) do not list *Idiospira* from the New York shallow marine communities, though Cooper (1956) cited its presence in the lower Trenton at Amsterdam. Strata around Paquette Rapids have common *Solenopora*, *Foerstephyllum*, and *Stromatocerium* which tend to indicate a late Blackriver or early Trenton age in the region.

Type materials. There are six syntypes in the Billings collection dated '1845': these types are GS1149, 1149*a–e*, only one of which corresponds to Billings's figure, except that the shell is damaged (pl. 1, figs. 21–25). This specimen, GS1149c, is selected as lectotype. The remaining specimens are all referable to *I. panderi*. All material from Paquette Rapids is partly or wholly silicified. In addition to the six syntypes, there were sixty-three

other topotype specimens from Paquette Rapids in the Royal Ontario Museum collection. These were variously labelled as *Camerella panderi* or *C. volborthi*. All specimens were larger than the Billings material, most of the larger specimens having been labelled *C. volborthi*, yet all specimens represented a clear growth gradient (text-fig. 9). A further collection of thirty-six specimens was made from the upper Napanee Limestone, about 1 km north of Napanee (NTS 31C/7W 44600:02920). Total 105 specimens.
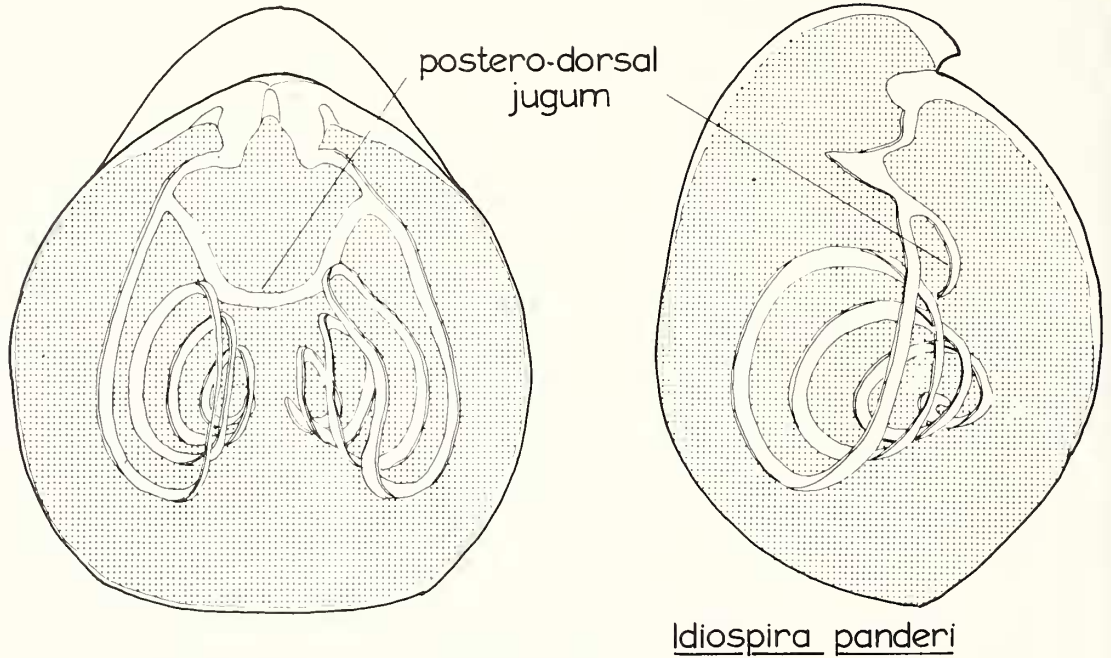
TEXT-FIG. 8. Brachidia of *Idiospira panderi* (Billings, 1859), based on text-fig. 10. Note the disposition of the jugum and spiralia. Scale × 8.

EXPLANATION OF PLATE 74

Figs. 1–5. *Idiospira panderi* (Billings, 1859). Hypotype ROM23918b, elongated specimen with high dorsal fold (compare with Pl. 73, figs. 31–35), × 3.

Fig. 6. '*Triplecella diplicata*' (Wilson, 1932). Holotype GS6659, single brachial valve in small limestone fragment. Lot 35, Concession 14, Charlottenburg Township near Ottawa, Ontario; Cobourg Fm., CF11, Caradoc, × 3. This species rests as a *nomen dubium* since only this fragment is known; very probably this is the dorsal valve of *Cyclospira bisulcata* (Emmons).

Figs. 7–21. *Cyclospira bisulcata* (Emmons, 1842). Two syntypes from the Emmons collection, and hypotype from the restricted type locality selected. Syntypes from Trenton Limestone, Adams, New York and hypotype from Gulfstream, near Rodman, NY; Hillier Mbr, Cobourg Fm., CF11, Onnian, Caradoc, × 3. 7–11, lectotype AMNH713-1a, well preserved specimen showing the double fold on the pedicle valve and bisulcate brachial valve. 12–16, paralectotype AMNH713-1b, a more quadrate specimen from the same locality. 17–21, hypotype GS59152, intermediate in shape between the two lectotypes and from Gulfstream locality.

Figs. 22–31. *Glassia elongata* Davidson, 1882. Specimens from Gotland, 6I Visby SO 'Djupvik 2' 55730:41660; Mulde Marl, late Wenlock, × 3. 22–26, hypotype Br106523, typical rounded specimen with small incurved beak. 27–31, hypotype Br106524, specimen with more strongly developed doubly sulcate commissure.

Figs. 32–36. *Peratos arrectus* n. gen. and sp. Eifel, Germany, MTB Dollendorf 53850:74680; Eilenberg Horizon, Freilingen Beds, late Eifelian, × 3. Hypotype GS59132, a typically sized specimen showing the development of a large interarea, deltidial plates and foramen.

PLATE 74

COPPER, Ordovician, Silurian, and Devonian atrypoids

Diagnosis. Moderately large for the genus, slightly longer than wide, ovoid, biconvex shells with anacline-hypercline beak, mostly smooth shell surface except for one or two lateral corrugations and a broad W-shaped dorsal fold. Internally shells have a broad, flattened U-shaped, postero-central jugum and dorso-medial spiralia of three to four revolutions.

Description. Shells are ovoid, elongate, somewhat globular but about 20 % of the shells are wider than long, more flattened and have less incurved beaks. Most shells have hinge angles of 85–95°, reaching maximum width anteriorly, with rounded commissure. Width peaks at 8–9 mm, lengths 9–10 mm, depths at 6–7 mm (text-fig. 9). Somewhat pointed beaks are incurved, but not completely hypercline early in growth, and the small pedicle opening and deltidial plates are usually obscured. Most shells have a broad dorsal fold with the crenulation in the middle producing a W-shape (rare shells lack this); the fold is flanked laterally by two short corrugations which begin late in shell growth (small shells being nearly smooth).
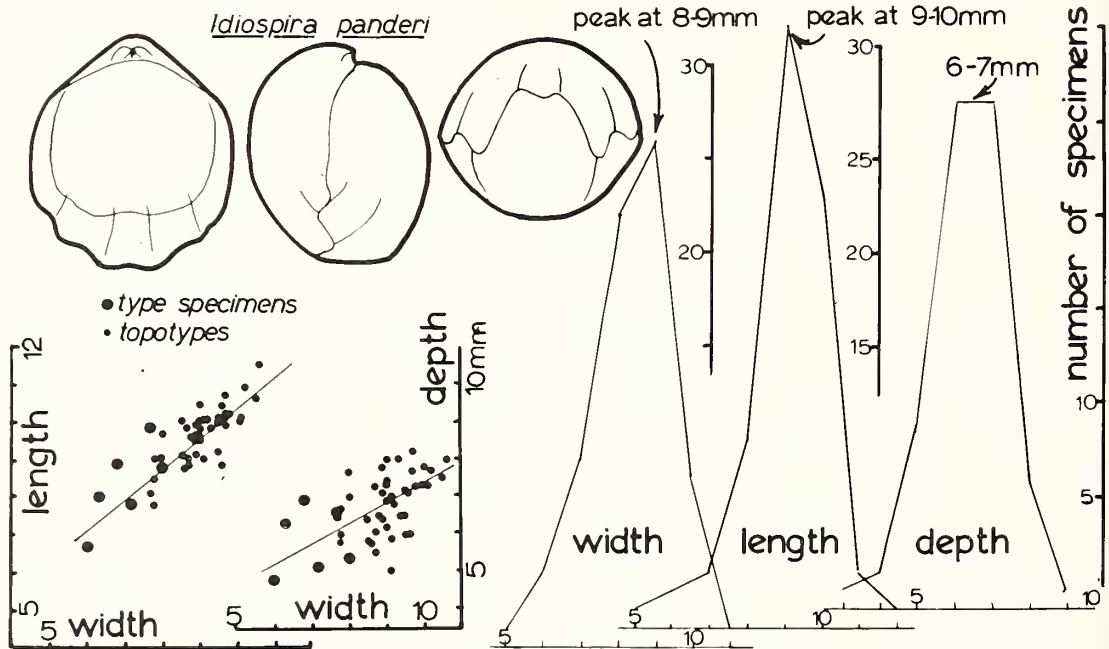
TEXT-FIG. 9. Scatter diagrams and frequency curves for *Idiospira panderi* (Billings, 1859) based on the type specimens and topotypes from the type locality at Paquette Rapids, Ontario (GS1149, ROM30884, ROM23920).

Internally, shells have no pedicle deposits, but large dental cavities, and small, hollow deltidial plates surrounding a minute foramen. Teeth are medially directed. Hinge plates are relatively thick, with a weak, striated cardinal process in the cardinal pit, bounded by a modest septum anteriorly. Small crural bases produce delicate crura which point ventrally, then laterally (text-fig. 10). The U-shaped jugum arises posteriorly and curves dorsally, ending as a flat shelf in the shell centre. Spiralial ribbons are tilted strongly to the shell middle but the cone axes point dorso-medially.

Remarks. The type species, *I. panderi*, is distinguished from *I. warthini* and *I. thomsoni* by its shape and presence of only one corrugation in the dorsal fold. Within the known succession of 'chronospecies' of *Idiospira* in Ontario, there is a general trend towards size increase, greater number of spiralial whorls and posterior-central migration of the jugum. Differences between species are apparently gradational.
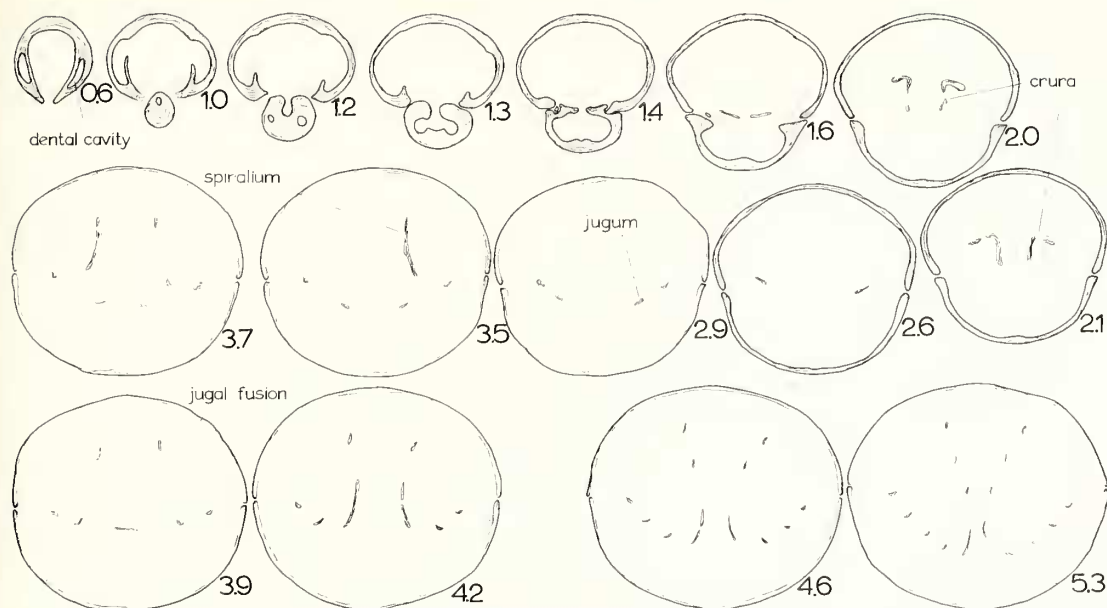
TEXT-FIG. 10. Serial sections of *Idiospira panderi* (Billings, 1859). Upper Napanee Limestone, Napanee, Ontario, NTS 31C/7W 444600:02930; Caradoc, CF8 to CF9. Specimen GS59080. Scale ×4.

Subfamily CYCLOSPIRINAE Schuchert, 1913 (emend.)

Diagnosis. Small, smooth, usually ventribiconvex to planoconvex, sulcate shells with normally thick, solid teeth, medially directed spiralia, no jugum.

Remarks. On the basis of broad similarity in shell morphology and apparent similarity in muscle scars to *Dayia*, Schuchert (1913), Schuchert and Cooper (1930) and Boucot *et al.* (1965) referred the genus *Cyclospira* to the family Dayiidae. *Dayia* and other Dayiinae like *Protozeuga* have a spiralium and jugum which is identical to those of the Hindellinae and Meristellinae. In addition the Dayiinae have laterally directed spiralia and are thus best relegated to the family Meristellidae (with nomenclatorial priority), and to the order Athyrida.

Cyclospira differs from athyroid brachiopods in having medially directed spiralia, and in having the spiralia located between diverging crura. In lacking any sign of a jugum or jugal processes it also differs from both athyroids and known atrypoids (thus far the only spire-bearer without this feature). *Cyclospira* seems an unlikely ancestor of the Athyrida, whose next oldest stratigraphic successor in North America is the Ashgill *Hindella*, since it would not only have to evert its spiralia but also 'grow' a jugum. Also, Fu (1982) reports a fully developed athyroid, *Apheathyris*, from late Caradoc strata of China. The median septum of *Cyclospira* is relatively long, reaching to mid-shell: this is a feature more common to some athyroids. The Cyclospirinae appear to have reached an evolutionary 'dead-end' in the Ordovician, and to have been an early, failed experiment in atrypoid filter-feeding strategy.

Genus *Cyclospira* Hall and Clarke, 1893
(= *Triplecella* Wilson, 1932; *Aulidospira* Williams, 1962)

Type species. Orthis bisulcata Emmons, 1842, p. 396, fig. 4, Hillier Limestone Mbr, Adams, New York; Caradoc, CF11.

Range. Late Caradoc–Ashgill. The lack of information on internal structure on many described species

makes it difficult to distinguish sulcate protozyginids from cyclospirinids and therefore to determine the exact range of the genus. Typical *Cyclospira* appear only in the late Caradoc (Actonian-Onnian, or Cobourgian in N. America), but the genus is absent to rare in Ashgill rocks of New York and Ontario. The genus has been reported by Foerste (1893) and Rubel (1977) from Early Silurian rocks, but these identifications are doubtful.

Diagnosis. Relatively small, smooth, ventribiconvex to planoconvex shells with a deep pedicle valve, weakly flattened, sulcate-bisulcate brachial valve and anacline to hypercline beak. Interior of shell very thick walled, solid teeth with slit-like dental cavities or dental nuclei. Small, medially oriented, weakly divergent crura, anteriorly continuous with medially pointed spiralia forming one to four coils; jugum lacking. Relatively long dorsal septum (text-fig. 11).

Remarks. The lack of a jugum is unique. It can be differentiated from *Manespira* and *Protozyga*, which may have a similar shape, by the thick apical shell wall, absence of large dental cavities and its relatively long dorsal septum. Twenty-five species have been assigned to the genus, and eleven more have been referred to other genera in the past. No doubt many of these are synonymous (see list below). Brachidia have been positively identified in only three species.

Species assigned. Cyclospira altunensis Liu, Zhang and Di 1984, p. 160, pl. 2, figs. 13–14. Mt Altun, China; Caradoc. This species is unusual in apparently possessing 'dental plates' and strong ribs on the anterior commissure. Brachidia unknown.

Cyclospira (?) *barrandei* Cooper, 1930, p. 281. A species based on illustrations of Barrande (1879, pl. 28, figs. II-3-16) from Czechoslovakia; late Ordovician. Ashgill(?). Brachidia unknown.

Cyclospira biloba Fu, 1982, p. 166, pl. 43, fig. 8*a–d*. Yueya Mountain, Ejina Qi, Inner Mongolia; Hengmanshan Fm., Middle Ordovician. Brachidia unknown.

Cyclospira(?) *canadensis* Cooper, 1930, p. 281, pl. 2, figs. 7–8. 'Dark shales in the road cut along Restigouche River, 3 miles above Matapedia', Quebec, Canada; late Ordovician. Brachidia unknown.

Protozyga carrickensis Reed, 1917, p. 945, pl. 24, figs. 30–31. Craighead Limestone, Craighead Quarry, Girvan, Scotland; late Caradoc (see Cocks 1978, p. 167). Brachidia unknown.

Merista cymbula Davidson, 1867, p. 204, pl. 22, figs. 28–29. Hendre-hen, Wales; Ashgill (see Cocks 1978, p. 168). Brachidia unknown.

Dayia cymbula var. *girvanensis* Reed, 1917, p. 948, pl. 24, fig. 33. Upper Drummock Group, Thraive Glen, Girvan; Rawtheyan, late Ashgill (see Cocks 1978, p. 168). Brachidia unknown.

Triplecella diplicata Wilson, 1932, pp. 399–400, pl. 5, fig. 13. 'Lower Cobourg Fm., east half of lot 35, Concession IX, Charlottenburg Township, in the creek bed'; late Caradoc. Only a single valve is known (see pl. 2). This is the type species of *Triplecella*. Wilson regarded the specimen as a pedicle valve, but Cooper (1956) viewed it as a brachial valve, placing it in synonymy with *Cyclospira*. If the specimen is indeed a pedicle valve, and this seems indeterminable because too little is preserved, then *Triplecella* could be a senior synonym of *Idiospira*. Cooper's concept is favoured. Brachidia unknown.

Cyclospira ejneqiensis Fu 1982, p. 166, pl. 43, fig. 9*a–d*. Horizon and locality as for *C. biloba* Fu, 1982. Brachidia unknown.

Cyclospira elegantula Rozman, 1964, pp. 188–189, pl. 23, figs. 4–5. Darpirskii Horizon, upper Kalychanskoi Suite, Selennyakh region, left bank Taryn-Yuryakh river, north-east USSR; Caradoc. In 1968, Rozman re-assigned the species to *Oligorhynchia*, but evidence seems inconclusive. Brachidia unknown.

Protozyga gastrodes Temple, 1968, pp. 53–55, pl. 10, figs. 1–12. 'Hirnantian limestones and mudstones above Keisley Limestone, lane near Keisley, Cumbria'. Strong ventral convexity, anterior sulcus and flat brachial valve point to *Cyclospira*. Brachidia unknown.

Cyclospira globosa Rozman, 1964, pp. 189–190, pl. 23, figs. 1–3. Kalychanskoi Suite, Selennyakh region, Kalychan, north-east USSR; early Ashgill (stratigraphically above *C. elegantula*). Brachidia unknown.

Cyclospira glansfagea Cooper and Kindle, 1936, p. 359, pl. 52, figs. 1, 4, 7. 'Rare in the crystalline limestone lenses on the southwest side of Priest's road', Percé, Quebec; Ashgill. Brachidia unknown.

Cyclospira levisulcata Roomusoks, 1964, pp. 12–13, pl. 4, figs. 6–10. Nabala Horizon, Lithuania; Harjuan, late Onnian–early Pusgillian, at Caradoc–Ashgill boundary. Brachidia unknown.

Cyclospira (?) *minuscula* Cooper, 1930, pp. 280–281, pl. 2, figs. 9–12. South Cove, locality F8, Percé, Quebec; Whitehead Fm., Ashgill. According to Cooper, 'spiralia indistinct, suggesting *Cyclospira*'.

Rhynchonella nana Davidson, 1869, p. 192, pl. 24, fig. 26. Killey Bridge Fm., Pomeroy, County Tyrone, Ireland; Cautleyan, middle Ashgill (see Cocks 1978). Brachidia unknown.

Camarella [*sic*] *owatonnensis* Sardeson, 1892, p. 328, pl. 14, figs. 1–3. '*Camarella* bed at Owatonna, Minnesota', probably Decorah Fm.: Trentonian, Caradoc. General shape suggests *Cyclospira*, but the shell is unusual in having lateral corrugations. Brachidia unknown.

Dayia pentagonalis Reed, 1897, p. 74, pl. 6, figs. 5, 5a–c. Keisley Limestone, Keisley, UK; Ashgill. See Cocks 1978, p. 168. Reed mentioned spiralia similar to *Dayia*, i.e. laterally directed, but this is questionable.

Protozyga perplexa Williams, 1962, p. 246, pl. 25, figs. 54, 55, 61, 62. Blue-grey mudstones of late Caradoc age overlying the Craighead Limestone, Craighead Quarry, Girvan (Cocks 1978). Brachidia unknown.

Cyclospira schucherti Roy, 1941, pp. 103–104, fig. 70. Frobisher Bay, Baffin Island; Caradoc. 'Spiralia are slightly introverted and nearly parallel to the vertical plane of the shell'. This indicates *Cyclospira*.

Cyclospira shaanxiensis Fu, 1982, p. 165, pl. 43, fig. 6a–d. Baiwangxilin Gou, Jingyang, Shaanxi Prov., China; Jinghe Fm., Middle Ordovician. Spiralia apparently directed postero-laterally with 2–4 revolutions.

?*Protozyga superba* Cooper, 1956, p. 686, pl. 141L, figs. 63–69. Auburn Chert, Missouri; upper Caradoc. Brachidia unknown.

Cyclospira tetraplicata Fu, 1982, pp. 165–166, pl. 43, fig. 7a–c. Hengliang Mtn., Tianzhu, Gansu, China; Goulang Fm., Middle Ordovician. Brachidia unknown.

Aulidospira trippi Williams, 1962, p. 253, pl. 25, figs. 44–46, 48, 49, 52, 56, 57. Kiln Mudstones, Craighead Quarry, Girvan; late Caradoc. I have examined the type materials; the 'shoe-lifter' process is a sparry calcite-mudstone grain boundary reflecting partial shell infill after death (i.e. a geopetal structure). Boucot *et al.* (1965) mention the lack of a jugum.

Cyclospira vokesi Roy, 1941, pp. 104–105, fig. 71. Locality and horizon as for *C. schucherti* of which it may be a population variant with weak ribs on the shell flanks. Caradoc. Brachidia unknown.

Dubious species. ?*Cyclospira circularis* Rubel, 1977, pp. 212–213, pl. 1, figs. 1–7. Lemmesk–Raikkiu Horizons, Estonia; middle Llandoverian. Brachidia unknown.

?*Cyclospira*(?) *sparsiplicata* Foerste, 1893, pp. 590–591, pl. 37A, fig. 18a–b. Huffman's Quarry, 'Clinton Group'; Llandoverian. Brachidia unknown.

Cyclospira bisulcata (Emmons, 1842)

Pl. 74, figs. 7–19; text-figs. 11–13

|	
1842	*Orthis bisulcata* Emmons, p. 396, figs. 4, 4a–c.
1847	*Athyris bisulcata* (Emmons); Hall, p. 139, pl. 33, fig. 3a–e.
1855	*Atrypa bisulcata* (Emmons); Emmons, p. 190, pl. 10, fig. 3a–e.
1894	*Cyclospira bisulcata* (Emmons); Hall and Clarke, p. 147, pl. 54, figs. 38–40.
1937	*Cyclospira bisulcata* (Emmons); Kay, pl. 10 (unnumbered fig.).
1946	*Cyclospira bisulcata* (Emmons); Wilson, pl. 11, fig. 1a–b.
1956	*Cyclospira bisulcata* (Emmons); Cooper, p. 693, pl. 142L, figs. 54–59.

Type locality. 'Adams, New York' (Emmons 1842); this locality is no longer exposed. Kay (1933, p. 7) found the species abundantly along Gulf Stream, near Rodman, NY; this material is almost identical to the type specimens. The measured section of Kay was re-collected: *C. bisulcata* is abundant in a 5 cm thick bed, along a bedding plane in the creek bed, about 30 m east of the bridge over Gulf Stream, 600 m east-north-east of Rodman, NY. This is selected as the restricted type locality.

Type horizon. 'Trenton Limestone' (Emmons 1842). Hall (1847, p. 139) mentioned 'shaly Trenton limestone, where few brachiopods occur'. Titus (pers. comm.) placed it in a 'shallow shelf facies'. The restricted horizon is the shaly part of the Hillier Limestone Mbr (upper Cobourg Fm.), about 10 m below the contact with the 'black shale of the Utica Fm' (Kay 1933, p. 7). The *Cyclospira* bed occurs in dark grey, thinly bedded, relatively barren micrite, and Kay (1937) stated it was also locally abundant in the underlying Steuben (Hallowell) Mbr of the Cobourg Fm. Both of these members lie within CF11 and are approximately equivalent to the uppermost Caradoc (Onnian), or lowermost *Pleurograptus linearis* zone.
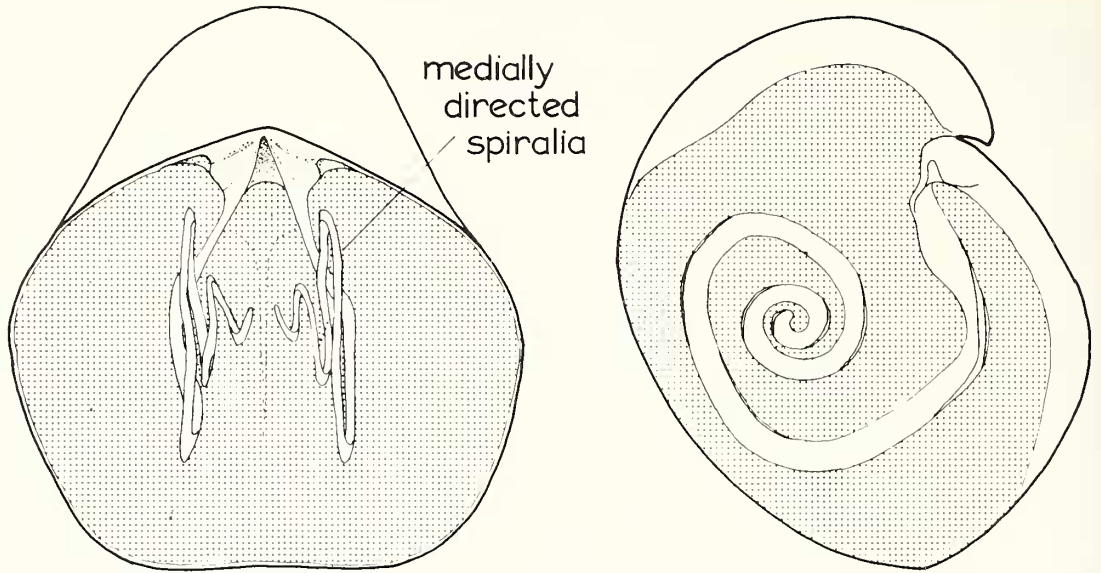
TEXT-FIG. 11. Brachidia of *Cyclospira bisulcata* (Emmons, 1842), based on text-fig. 13. Note the medial direction of spiralia and absence of a jugum. Scale × 10.
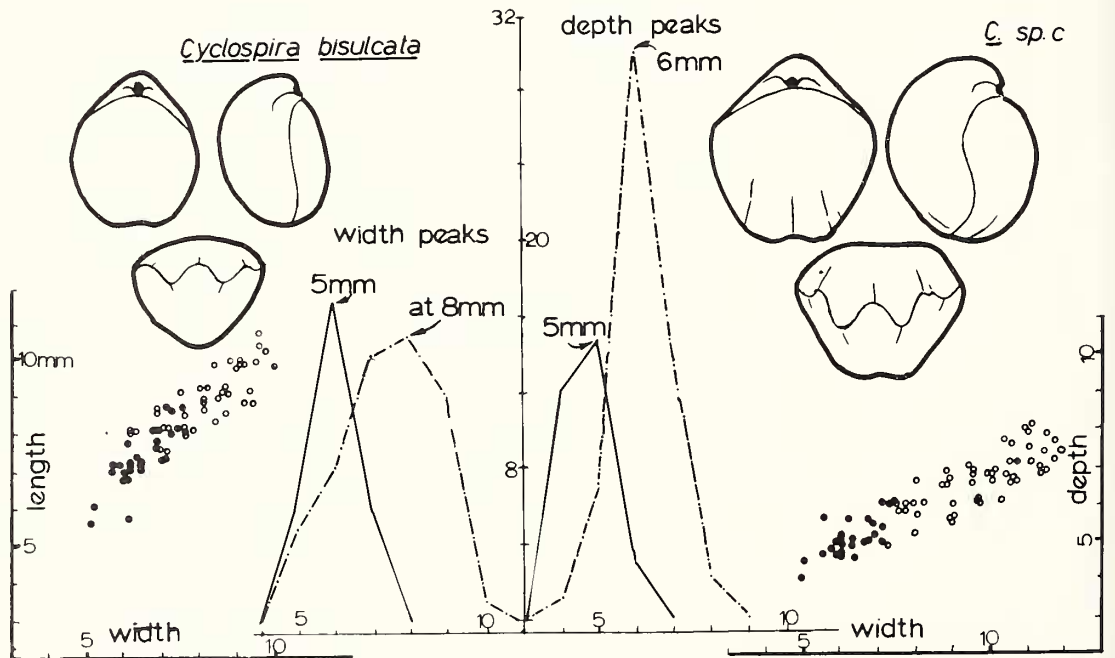

TEXT-FIG. 12. Scatter diagrams and frequency curves comparing *Cyclospira bisulcata* (shown on left, solid dots, solid lines) from Gulf Stream, NY with an undescribed sp. C (circles, dashed line) from the upper Cobourg Fm., Craigleath, Ontario which is believed to represent a stratigraphically younger form (high CF11).

Type material. Two syntypes from the Emmons collection in the American Museum of Natural History (AMNH), New York. AMNH713-1a is selected as lectotype; AMNH713-1b is a paralectotype. In addition more than fifty well-preserved specimens were collected at Gulf Stream, NY; two specimens from the Escanaba River, Cornell, Michigan (ROM24219); twenty specimens from 'Cobourg Fm., Ottawa' (ROM18913).

Diagnosis. Small, slightly elongated, ventribiconvex shells with narrow hinge, inflated, angular umbo, foramen expanded into umbo, strongly incurved beak and bisulcate commissure. Internally thick-shelled, narrow, slit-like dental cavity or dental nucleus, strong, rectangular muscle pad and stout, solid teeth. Dorsally, a distinct, long, median septum (nearly one-third shell length), arcuate crural bases extending into crural blades which are trough-like anteriorly; spiralia of two or three medially directed whorls (text-fig. 11).

Description. Shells relatively small for the genus (average width 6 mm, length 7 mm, depth 4–5 mm; w/l ratios 0·85–0·89 (text-fig. 12). Apical angle about 70–80°. Umbo inflated, beak hypercline, foramen normally breaking into umbo with small, wide flanks adjacent to umbo. Ventral valve strongly inflated, dorsal valve flattened; commissure bisulcate. Internally, apical ventral cavity squared, with weakly indented sides; rounded double muscle pad posteriorly, weak groove anteriorly. Teeth dorso-medial, with stubby sides, pointed ends. Dorsal cardinalia thickly reinforced, crura delicate, arched ventrally and laterally; spiralia with two or three whorls located ventrally, directed to centre (text-figs. 11, 13).
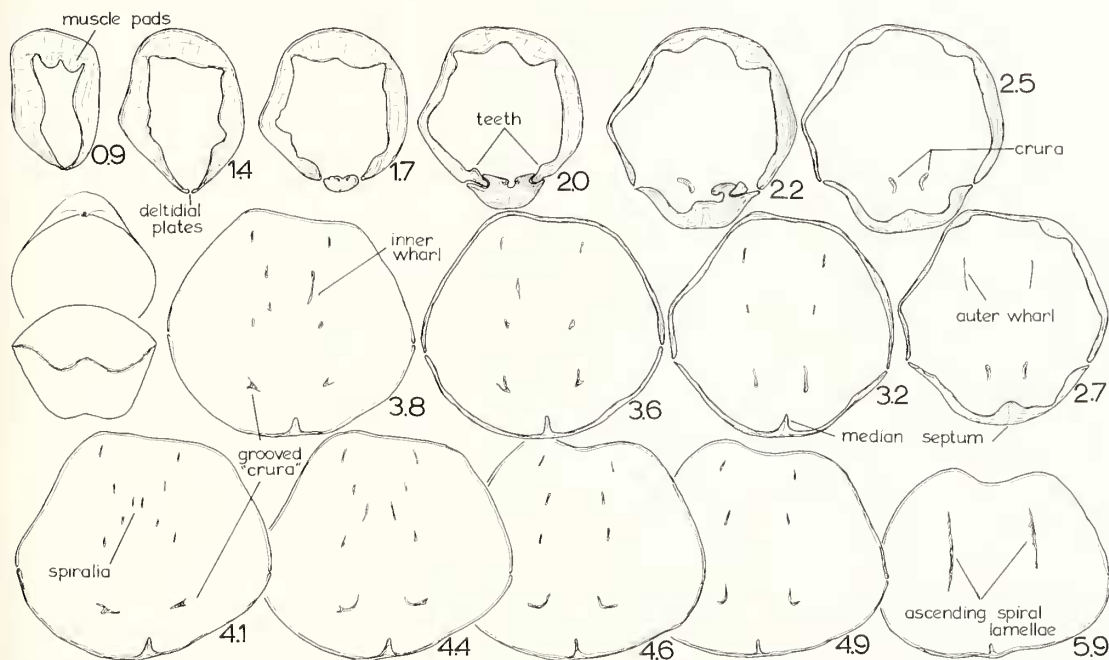
TEXT-FIG. 13. Serial sections of *Cyclospira bisulcata* (Emmons, 1842) from the designated type locality, 600 m east-north-east of Rodman, along Gulf Stream, NY; Hillier Mbr, Cobourg Fm., late Caradoc, lower CF11. GS79442. Scale × 5.

Remarks. *C. bisulcata* occupies a relatively intermediate position in terms of shell size, being smaller than *C. schucherti* Roy, 1941, which at 12 to 13 mm is large for the genus. It differs from other species in its bisulcate commissure, and distinctive shell shape. Evolutionary trends in the known species are not possible to establish at present.

Subfamily GLASSIINAE Schuchert and Levene, 1928

Diagnosis. Relatively thick-shelled, normally biconvex, smooth atrypoids with medially directed, barrel-shaped spiralia, separated jugal processes, and incipient or fully developed dental plates.

Remarks. This subfamily is unique amongst the Siluro-Devonian spire-bearers for possessing medially directed spiralia (text-fig. 14). The oldest known spire-bearing brachiopods, including Ordovician taxa such as *Manespira*, *Protozyga* and *Cyclospira* also developed medially directed spiralia, but this is seen as the 'starting point' for spiralia, and thus a primitive trend. Medial orientation places an immediate constraint on expansion of the spiralia, as the growing apices would meet in the shell centre. With lateral spiralia, expansion occurs alongside lateral shell growth (as seen in *Spirifer*), and with dorsal spiralia alongside brachial valve globosity (as seen in *Atrypa*). Hence the Glassiinae tended to be small-sized, rarely exceeding 15 mm in width except in Middle Devonian time. Similarly, the spiralia of Glassiinae tend to be barrel-shaped instead of conical (accommodating shell convexity), with the shell commonly being pinched (or bisulcate) in the centre, reflecting spiralium shape.

The subfamily was initially erected to include only a single genus, *Glassia*. The subfamily status was dropped by Siehl (1962), who assigned *Glassia* to the Lissatrypinae, elevated to family status by Rzhonsnitskaya (1964), only to be dropped once more in the Treatise (Boucot *et al.* 1965), who assigned these to the Septatrypinae. Three other genera are here assigned to the Glassiinae: *Karbous* Havlicek, 1985 (which has shell structure and dental plates like some *Glassia*), *Peratos* n. gen. and, questionably, the genus *Holynatrypa* Havlicek, 1973, for which brachidia are still undescribed (but which were stated by Havlicek to have medial spiralia).

Genus *Glassia* Davidson, 1881
(= *Cryptatrypa* Siehl, 1962)

Type species. *Atrypa obovata* Sowerby, 1839, p. 618, pl. 8, figs. 8–9. 'Mathon Lodge, west flank of Malvern Hills', England; 'Lower Ludlow rock'.
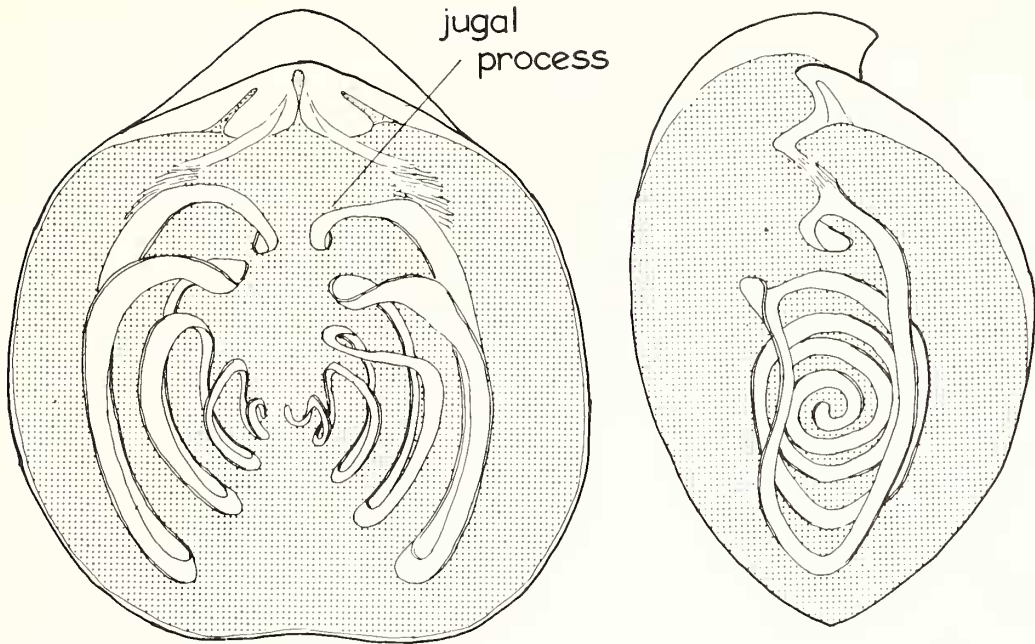
Range. ?Middle Llandoverian, Wenlock–Ludlow, ?Pridoli.

Distribution. North-west Europe, Central Asia?, China?, Australia, north-west Canada? (the only definitive Glassiinae to date are known from north-west Europe).

Diagnosis. Small- to medium-sized, biconvex, smooth, rounded shells, possessing anacline-hypercline beaks, small apical or trans-apical foramen, deltidial plates and small interarea; rectimarginate or bisulcate. Internally thick-shelled, with minute posterior dental cavity filled in anteriorly to produce stout, solid teeth with an inner, buried, thin, dental plate. Dorsal valve with stout hinge plates, narrow cardinal pit, small crural bases, rapidly diverging distally feathered crura. Jugal processes ventro-posterior, arched centrally, terminating in small jugal plates which nearly touch to form an O-structure. Spiralia medial to ventro-medially directed with posterior parts of whorls trough-shaped, directed to jugal processes (text-figs. 14, 15).

Remarks. *Glassia* is similar to its Devonian descendant, the genus *Karbous* Havlicek, 1985, in it biconvexity, small anacline beak and interarea, but differs internally by its absence of dental cavities and perhaps by its modest jugal plates (since these are undescribed for *Karbous*). *Glassia* differs from Middle to Late Devonian *Peratos* n. gen. in its incurved beak and lack of prominent dental plates and large dental cavities. There was a trend in the Glassiinae towards increasing the size of the interarea, developing an orthocline beak, and enlarging the dental cavities and the jugal plates.

The genus *Holynatrypa* Havlicek, 1973, from Emsian–Eifelian strata of Czechoslovakia, was said to have 'spiralia probably directed medially'. If this is correct, it must belong to the Glassiinae, but the beak is minute and shell shape resembles *Lissatrypa*. It is a doubtful glassiinid and probably a *Lissatrypa*.
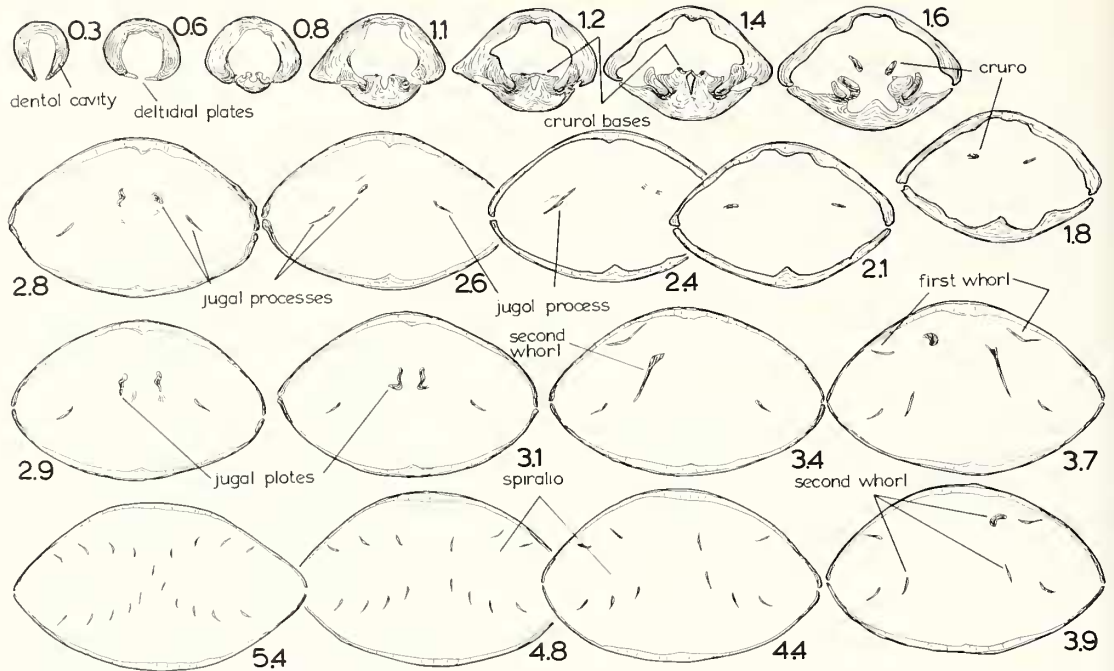
TEXT-FIG. 14. Brachidia of *Glassia elongata* Davidson, 1881, based on text-fig. 15. Note that crura are fibrous, jugal processes separated and spiralia curved in the centre. Scale × 8.

The genus *Spondylobolus* M'Coy, 1851 (type species *S. craniolaris* M'Coy, 1851) is probably a senior synonym of *Glassia* Davidson, 1881. The name has been used only twice in the literature; firstly by Salter (1873, p. 135), who stated 'a genus unfortunately founded in mistake; a species of *Meristella*, probably *M. obovata* being so pressed in shale . . . ', thus recognizing its identity with *Glassia* and the senior synonym status of the genus *Spondylobolus*. This was re-asserted by Cocks (1978, p. 160). The name *Spondylobolus* should be suppressed because it would create substantial confusion in the literature.

The Ludlovian genus *Quangyuania* Sheng, 1975 from China superficially resembles *Glassia*, but figures of the type species, *Q. ovalis*, indicate teeth, crura, spiralia, and a dorsal septum as in *Lissatrypa*, which is probably a senior synonym. Similarly, the Ludlovian genus *Buceqia* Havlicek, 1984, type species *Terebratula obolina* Barrande, 1847, is, from the serial section data provided by Havlicek, internally identical to *Lissatrypa* Twenhofel, 1914, and is here regarded as a junior synonym thereof.

The first evidence for the unique medial orientation of the spiralia in *Glassia* was provided by Kunth (1865), who examined and illustrated spiralia from *Glassia* found in Silurian glacial erratics in North Germany (derived from Gotland: see also Gagel, 1890, pl. 1, fig. 38). This was confirmed by the work of Glass (in Davidson 1881a, b), which led to the founding by Davidson of the genus. Glass was remarkably accurate in his work but for showing a jugum, instead of disconnected jugal processes. The oldest known, possible *Glassia* is *G. mogoktaensis* Nikiforova 1961, for which Modzalevskaya (in Nikiforova 1961) showed medial spiralia. *Glassia* may have evolved from either *Meifodia* or *Lissatrypa*. Some twenty species have been assigned to the genus, but for most the brachidia are unknown; there may be substantial synonymy. Four species previously assigned have been removed.

TEXT-FIG. 15. Serial sections of *Glassia elongata* Davidson, 1881 from the lower Mulde Beds, Djupvik 2, 6I
Visby SO 41660:55730, Gotland, Sweden; middle Wenlockian. A dental cavity is present posteriorly, but
dental plates are absent; spiralia are barrel-shaped instead of conical. GS79444. Scale ×4.

Species assigned. ?*Atrypa canaliculata* Barrande, 1879, pl. 15, figs. 1, 1–4; pl. 145, figs. lII–VII. 'Dlauha Hora,
Etage E–F', Kopanina Fm.; Ludlovian (*non Collarothyris canaliculata* Venyukov, 1899).

?*Terebratula cingulata* Meyer and Münster, 1840, pp. 77–78, pl. 14, figs. 12, 13*a–b*. 'Orthoceratitenkalk von
Elbersreuth', Germany; Wenlock–Ludlow. Brachidia unknown.

Atrypa compressa Sowerby, 1839, p. 629, pl. 13, fig. 5 (both views). 'Woodside and Nash, near Presteign';
Wenlock shales. Usually regarded as a synonym of *G. obovata*.

Spondylobolus craniolaris M'Coy, 1851, p. 408 (figured in M'Coy 1855, p. 255, pl. 1H, figs. 4–5). 'Black shale
of Builth Bridge', Powys, UK; Wenlock Shales. A probable senior synonym of *G. obovata*. It should be
declared a *nomen nudum*.

Atrypa decapitata Heritsch, 1929, p. 8, 'E2 von Bohmen (Kozel)'. This has sometimes been cited as a *Glassia*
but the name appears invalid (no figures are known).

Glassia elongata Davidson, 1881*b*, pp. 148–149, pl. 5, figs. 3–4. 'Railway cut between Tickwood and Farley
Dingle' (Davidson 1881*a*, p. 103), Wenlock Edge, Salop; Coalbrookdale Fm., formerly Tickwood Beds
(Sheinwoodian–Homerian: Wenlock). This is a common species in Gotland (see pl. 2, figs. 22–31; pl. 3, figs. 2,
7; text-figs. 14–15). It may be a synonym of *Atrypa laevigata* Kunth 1865.

?*Terebratula ephemera* Barrande, 1847, p. 408, pl. 16, fig. 11*a–e*. 'Grenze . . . unteren und mittleren Kalketage
E und F in den Umgegenden von Beraun und St. Iwan'; Ludlovian–Pridolian. Brachidia unknown.

?*Atrypa fugitiva* Barrande, 1879, pl. 84, figs. V, 1–3; pl. 136, Figs. III, 1–2. 'Dlauha Hora . . . Kolednik, -E2';
Ludlovian. Brachidia unknown.

?*Atrypa fugitiva* Barrande var. *depressa* Vinassa de Regny, pp. 557–558, pl. 20, fig. 6*a–b*. Volaia, Carnic Alps,
Italy, 'Calcari con crinoidi *e Retzia* (= *Gracianella*) *umbra*'; Pridolian. Brachidia unknown.

?*Cryptatrypa glaberconcha* Lenz, 1977, p. 1550, pl. 12, figs. 1–13. 'Locality 2, approximately 6 miles east of

Avalanche Lake, Mackenzie Mountains, 90–99 m below section top, Whittaker-Road River formations transition'; early Wenlock. Brachidia unknown.

?*Spirigera heimoi* Heritsch, 1929, p. 34, pl. 3. figs. 145–150. 'Rotenkalk', Kokberg, Carnic Alps, Austria; Ludlovian. Brachidia unknown.

?*Australina (Australina) krausi* Strusz, 1982*b*, pp. 123–126, figs. 19–20. Mudstone in the Walker volcanics, Molonglo Valley west of Canberra, Australia; Wenlockian. Brachidia unknown. Biconvexity and interarea suggest *Glassia* but internal structures are unknown.

Atrypa laevigata Kunth, 1865, p. 313, pl. 7, fig. 1*a–e*. 'Graptolithengestein, Tempelhof, Berlin'; Ludlovian (specimens from glacial erratics probably derived from Gotland to the north). Figures were later copied by Heidenhain (1869, p. 155) and Roemer (1885, pl. 9, fig. 11). Spiralia medially directed.

?*Atrypa lindstroemi* Venyukov, 1899, pp. 122–123. Studenitsa Limestone, Studenitsa, Podolia; Wenlockian. Brachidia undescribed.

?*Glassia minuta* Rybnikova, 1967, pp. 203–204, pl. 23, fig. 3*a–f*. Kholdve, Latvia; Llandoverian. May be a *Lissatrypa*. Brachidia unknown.

?*Glassia minuta* Fu, 1982, pl. 42, fig. 13*a–d*. Shimen valley, Zhouqu, Gansu, China; Zhouqu Fm., Wenlock. Spiralia undescribed.

Glassia mogoktaensis Nikiforova, 1961, pp. 250–252, pl. 52, figs. 10–16. Mogokta River, Khantaiki River basin, north-west Siberia; middle Llandoverian. Medially directed spiralia present (ibid., text-fig. 44), jugum unknown.

?*Karpinskia nalivkini* Nikiforova, 1937, p. 23, pl. 2, figs. 4–5. Outcrop 723, western Balkhash, central asiatic USSR; Wenlockian. Brachidia unknown.

Terebratula philomela Barrande, 1847, p. 387, pl. 15, fig. 7. 'Letzten Schichten unseren Kalketage E . . . und höchste Entwicklungstufen in dem untern Theil unseren mittleren Kalketage F', no locality cited. According to Havlicek (1985) this species is of Wenlock age (Motol Fm.).

?*Cryptatrypa praecordata* Kulkov, 1974, pp. 69–70, pl. 23, fig. 7, pl. 24, fig. 1. South-west Altai, Gora Rosypnaya, Talyi, Chinetinsk Horizon, Yavorski Fm.; upper Llandoverian. Brachidia unknown.

?*Nucleospira raritas* Amsden, 1968, p. 157, pl. 8, fig. 8*a–h*. Batesville District, Arkansas, St Clair Limestone; Ludlovian. Brachidia unknown. This occurrence, if correct, would be anomalous since no other *Glassia* are known from eastern North America.

?*Glassia rotunda* Rybnikova, 1967, pp. 201–202, pl. 23, fig. 2*a–f*. Piltene, Latvia; *Pristiograptus tumescens* Zone, Ludlovian. Brachidia unknown.

?*Cryptatrypa rotunda* Lenz, 1977, pp. 1550–1552, pl.12, figs. 14–27. Locality and horizon as for *C. glaberconcha* Lenz, 1977. Brachidia unknown; a homonym of *G. rotunda* Rybnikova.

Atrypa subcompressa mut. *progona* Frech, 1887, p. 727. 'Vorkommen in der Zone der *Rhynchonella megaera* am Wolayer Thörl'; ? Pridolian. Brachidia unknown.

Species deleted or dubious. Glassia drevermanni Mailleux, 1936, referred to *Peratos* n. gen.

Cryptatrypa fahraeusi Lenz, 1970, pp. 492–493, pl. 86, figs. 11–24, 26, 28. 'Upper part of the Road River Formation, Prongs Creek, Yukon'; Pridolian. Very large dental cavities and shell form appear to indicate *Septatrypa*. Brachidia unknown.

Glassia minuscula Dahmer, 1932, referred to *Karbous*.

Terebratula obolina Barrande, 1847, pp. 404–405, pl. 20, fig. 16*a–e*. 'Kalkbänken mit *Phacops glöckeri* und *Arethusa koninckii*' near Beroun, Czechoslovakia; Wenlockian. Havlicek (1984) has demonstrated dorsally directed spiralia and internal structure like *Lissatrypa*, but assigned it to a new genus, *Buceqia*.

Glassia paucicosta Spriestersbach and Fuchs, 1909, referable to *Karbous*?

?*Glassia romingeri* Hall and Clarke, 1894, referred to *Idiospira*.

Glassia sulcata Siehl, 1962, referred to *Peratos* n. gen.

?*Glassia tenella* Williams, 1951, pp. 114–115, pl. 5, figs. 16–18. 'Mountain road almost half a mile SSW of Cwm Crychan, north-east of Llandovery'; Llandoverian. The cardinalia shown resemble those of *Lissatrypa*. Brachidia unknown.

Cryptatrypa triangularis Johnson, Boucot and Murphy, 1976, pp. 75–76, pl. 25, figs. 22–30; pl. 26, figs. 1–4. 'B fauna, Pete Hanson Creek area', Alaska; Ludlovian. Brachidia unknown. The peculiar triangular shape of this species suggests possible affinity with *Eokarpinskia nalivkini* (Nikiforova 1937), the type of the genus (Rzhonsnitskaya 1964), a smooth or nearly smooth brachiopod whose brachidia are unknown. *E. nalivkini* was described by Lenz (1970) as a *Cryptatrypa*. Lenz's species is similar to *Terebratula baucis* Barrande, 1847, whose internal structure is still unknown. None of these are specifically referable to the subfamily Glassiinae.

Glassia variabilis Whiteaves, 1904, pp. 42–43; Whiteaves 1906, pp. 273–274, pl. 26, figs. 3–5. 'Loose blocks of limestone from or near the mouth of the Winisk River', Hudson Bay Lowlands, Ontario; Wenlockian. Types re-examined: spiralia dorsal and specimens referred to *Atrypopsis*.

Genus *Karbous* Havlicek, 1985

Range. Gedinnian (Lochkovian)–Dalejan (Lower Devonian, possibly lowest Eifelian).

Distribution. North-west Europe, Urals, ?central Asia.

Emended diagnosis. Small to medium-sized, smooth, ventribiconvex to planoconvex shells with relatively prominent incurved beak, hidden foramen, solid deltidial plates, usually rectimarginate or weakly bisulcate. Internally thick-shelled, with small, short, dental plates flanked by small, slit-like dental cavities. Dorsally thick, disjunct hinge plates. Crura and spiralia yet undescribed or figured.

Remarks. The genus differs from *Glassia* in having a clearly defined dental plate and usually a narrow, slit-like dental cavity (Siehl 1962, has shown that the dental cavity may be filled in but that the dental plate is still clearly developed as a single crystal structure within the teeth). In *Glassia* there is a thin lining to the pedicle cavity (pl. 75, fig. 1; text-fig. 17) and an apical dental cavity lining, the precursors of dental plates in *Karbous*. *Karbous* differs from *Peratos* in having an incurved beak and small dental cavities.

Species assigned. ?*Atrypa canaliculata* var. *dissidens* Barrande, 1879, pl. 146, figs. I, 1–2. 'Konieprus, Etage F', Czechoslovakia; Pragian, Devonian. Brachidia unknown.

?*Cryptatrypa curvirostris* Xu, 1979, p. 374, pl. 4, figs. 22–28. Luofu, Nandan, Guangxi Province, south-west China; late Emsian–early Eifelian. Brachidia unknown.

?*Atrypa insocia* Barrande, 1879, pl. 147, fig. 1. 'Konieprus, Etage F'; early Devonian. Brachidia unknown.

?*Glassia minuscula* Dahmer, 1922, pp. 287–288, pl. 15, figs. 23–25. 'Giengelsberger Schichten', Giengelsberg, Germany; Emsian. Brachidia unknown: appearance possibly suggests the anoplothecid athyroid *Dnestrina*.

?*Glassia paucicosta* Spriestersbach and Fuchs, 1909, pp. 68–69, pl. 10, figs. 3–4. Dalhausen, Germany, Remscheider Schichten; upper Emsian. Brachidia unknown.

Karbous truncatus Havlicek, 1985, pp. 237–238, pl. 2, figs. 3–4. Suchomasty Limestone (Dalejan; Emsian); Herget Quarry, Koneprusy, Czechoslovakia.

Karbous vaneki Havlicek, 1985, p. 238, pl. 1, figs. 1–2. Zlichov Limestone, Zlichovian, Lower Devonian; Koneprusy area.

Species deleted. *Cryptatrypa lenticula* Perry 1984, pp. 105–106, pl. 40, figs. 1–27. 'Locality S3, East limb of Sekwi Anticline, north-north-west of Natla River, 161·5–164·6 m level below top of Delorme Fm'; Zlichovian. In this posthumous manuscript Perry illustrated laterally directed spiralia which are unmistakably athyroid; the species is best assigned to *Protathyris*.

Atrypa subcompressa Frech 1887, pp. 726–727 (designated for figures in Barrande, 1879, pl. 85, fig. 1; pl. 114, fig. 4), 'Konieprus', Czechoslovakia; Lower Devonian. Barrande's figures show laterally directed spiralia, and this is thereby an athyroid.
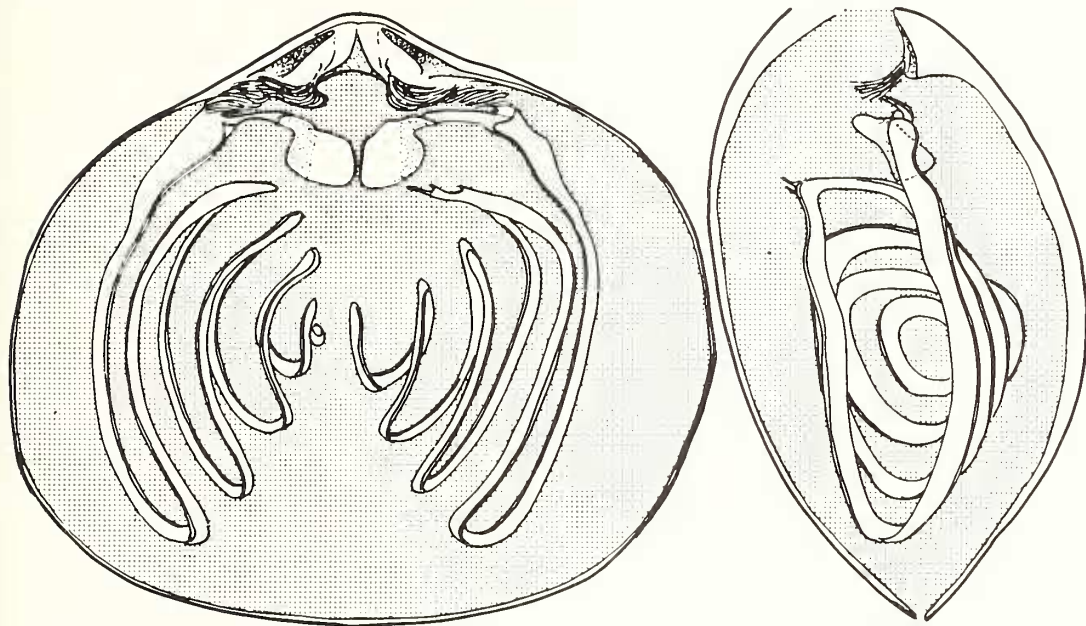
Genus *Peratos* n. gen.

Name. From the Greek, *peratos*, meaning the end of the line, referring to the fact that this genus is the last occurrence of the Glassiinae.

Type species. Peratos arrectus n. sp. Eilenberg Horizon, Freilingen Beds, late Eifelian; Eifel, Germany.

Range and distribution. Eifelian–Frasnian, Devonian; north-west Europe.

Diagnosis. Relatively large glassiinids with a biconvex shell, prominent interarea with erect, ortho-cline beak and large, exposed pedicle foramen. Internally with long, straight, flat dental plates and very large dental cavities. Delicate crura feathered distally, short jugal processes giving rise to highly arched jugal plates producing a trough structure. Spiralia medially directed as in *Glassia* and possessing spines anteriorly (text-figs. 16 and 17).

TEXT-FIG. 16. Brachidia of *Peratos arrectus* n. gen., n. sp., based on text-fig. 17. Note the large jugal plates. Scale ×8.

Remarks. This genus differs externally from other members of the subfamily in having a large, orthocline beak and relatively large interarea. On the inside it has long and straight dental plates defining a large, open dental cavity behind them. Spiralia are identical to those of *Glassia*, i.e. barrel-shaped and medially oriented, but the jugal processes are quite different.

The presence of dental plates in Devonian *Cryptatrypa* (here identified as *Peratos*) led Siehl (1962), who did not find spiralia, and Boucot *et al.* (1964), to place such shells in the family Septatrypinae. But the overall shell wall and hinge structures of *Glassia*, *Karbous*, and *Peratos*, and especially the peculiar spiralia (text-fig. 16), show that the three are related. In *Glassia* there is a thin lining to the pedicle cavity (pl. 75, fig. 1; text-fig. 17) and an apical dental cavity lining, signalling dental plates in both *Karbous* and *Peratos*.

Peratos is most common in calcarenites associated with reef development in the Devonian. Silurian *Glassia* are more common in dark gray to black calcareous shales or micritic limestones representing offshore environments. It is possible that this represents a change in habitat in the Glassiinae from Silurian to Devonian time. There appears to be strong homeomorphy between *Peratos*, Devonian athyrids like *Protathyris*, and centronellid brachiopods, which makes it difficult to assess described species in the literature unless the brachidia are known. About thirteen species of probable or possible *Peratos* have been described.

Species assigned. Rhynchonella beyrichi Kayser, 1872, p. 678, pl. 26, fig. 6*a–k*. 'Rotheisenstein', red limestone, Brilon, Germany; late Givetian or Frasnian. Refer to Maurer (1885, pp. 192–193, pl. 8, figs. 11–15), who illustrated the medially directed spiralia, Torley (1934, p. 125, pl. 9, figs. 78–79) and Gunia (1962, p. 511, pl. 47, figs. 11–12) for additional material. Serial sectioning by me of Brilon specimens shows medially directed spiralia and internal structures like the type species.

?Atrypa canaliculata Barrande, var. 1 Maurer 1881, p. 38, pl. 2, fig. 23*a–c*. Herborn, Germany, Greifensteinerkalk; Eifelian. Brachidia unknown.

?Atrypa canaliculata Barrande, var. 2 Maurer 1881, p. 39, pl. 2, fig. 24*a–c*. Locality and horizon as for var. 1.
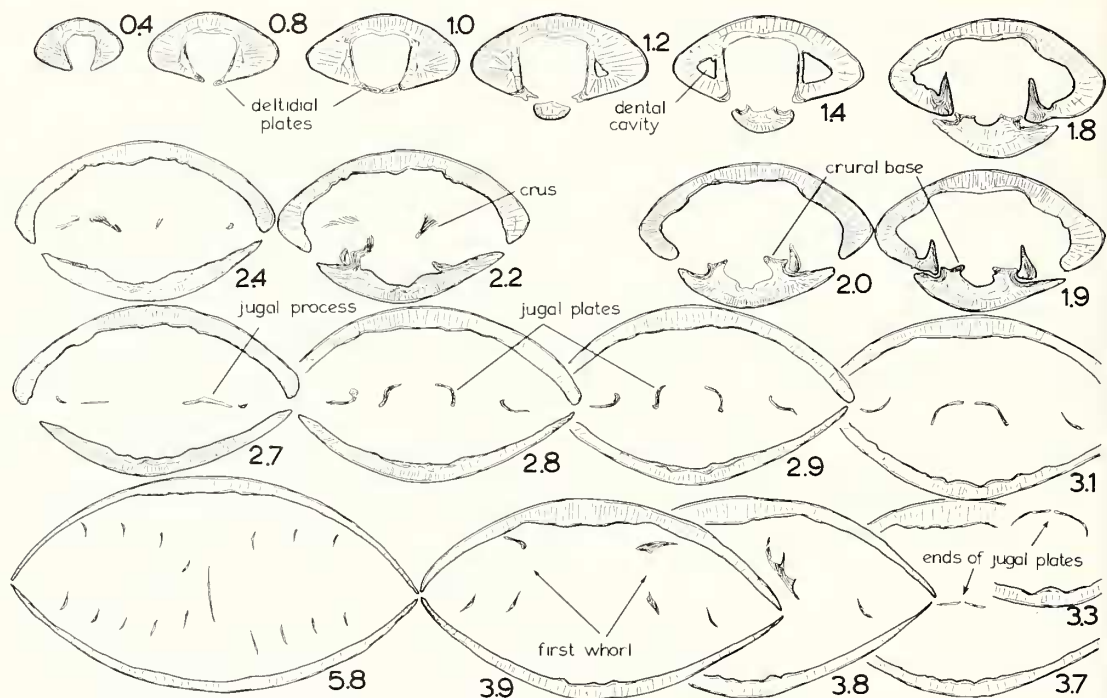
TEXT-FIG. 17. Serial sections of *Peratos arrectus* n. gen., n. sp. from the Eilenberg Horizon, Freilingen Beds, MTB Dollendorf 53850 : 74680, Eifel, Germany; late Eifelian. Note the dental plates and dental cavity and unusual jugal plates. GS59133. Scale ×4.

?Glassia drevermanni Mailleux, 1936, p. 25 (no figs.). 'Les schistes de Matagne', Couvin and Sautour, Belgium; Frasnian F3b. Brachidia unknown.

Cryptatrypa hassiaca Siehl, 1962, pp. 198–199, pl. 27, figs. 5–6, pl. 37, figs. 4, 6. 'Schurf in der Wiege, Greifenstein, Schicht 17.0 m Greifensteinerkalkes'; upper Eifelian. Brachidia unknown.

?Terebratula newtoniensis Davidson, 1867, pp. 8–9, pl. 1, figs. 16–17. Lane's or Woolborough Quarry, Newton Abbot; Middle Devonian. These are very large shells and may belong to early terebratulids.

Cryptatrypa philomela minor Biernat, 1966, p. 110. Holy Cross Mountains, Poland, Skala Beds; Givetian.

?Terebratula puschiana Verneuil, 1845, pp. 69–70, pl. 9, fig. 10*a–e*. 'À Ulahue, entre Krapivna et Odoieff, sur la route de Toula à Kalouga'; ?Upper Devonian. Compared by Verneuil to *Glassia obovata*, but brachidia unknown.

?Camarophoria rhomboidea Phillips, in Tietze 1871, p. 151, pl. 17, figs. 41, 41*a*. 'Hauptkalk, Ebersdorf', Germany; Middle Devonian. Brachidia unknown.

?Terebratula rotundata Meyer and Münster, 1840, p. 75, pl. 14, fig. 3*a–b*. 'Clymenienkalk von Schübelhammer', Germany; Frasnian. This species was cited by Drevermann (1901, p. 168) and Gunia (1968, p. 166, pl. 7, fig. 17*a*). Brachidia unknown.

Glassia sulcata Siehl, 1962, pp. 194–195, pl. 25, figs. 2–4; pl. 37, figs. 1–3. 'Schurf in der Wiege, SW Griefenstein . . . Schicht 5·20 m des Greifensteinerkalkes'; upper Eifelian.

Atrypa verrucula Maurer, 1881, pp. 43–44, pl. 3, fig. 9*a–c*. Griefensteinerkalk, Herborn, Germany; Eifelian. Serial sections by Siehl (1962) indicate the genus *Peratos*.

Glassia whidbornei Davidson, 1882, pp. 38–39, pl. 1, figs. 10–14. 'Middle Devonian limestone at Lummaton, England; Late Eifelian or Givetian. Brachidia medially directed.

Peratos arrectus n. sp.

Pl. 74, figs. 32–36; Pl. 75, fig. 1; text-figs. 16, 17

Name. Latin *arrectus*, referring to the large, upright beak.

Type locality and horizon. Small roadcut in the Hillesheim Syncline, Eifel, MTB Dollendorf 53850:74680; Eilenberg Horizon, Freilingen Beds, Late Eifelian.

Diagnosis. Shell medium-sized, rounded in outline, 12–15 mm wide, equidimensional or slightly longer than wide, biconvex, with orthocline beak and hinge angle averaging about 110°. Internal structures as shown in text-figs. 16 and 17.
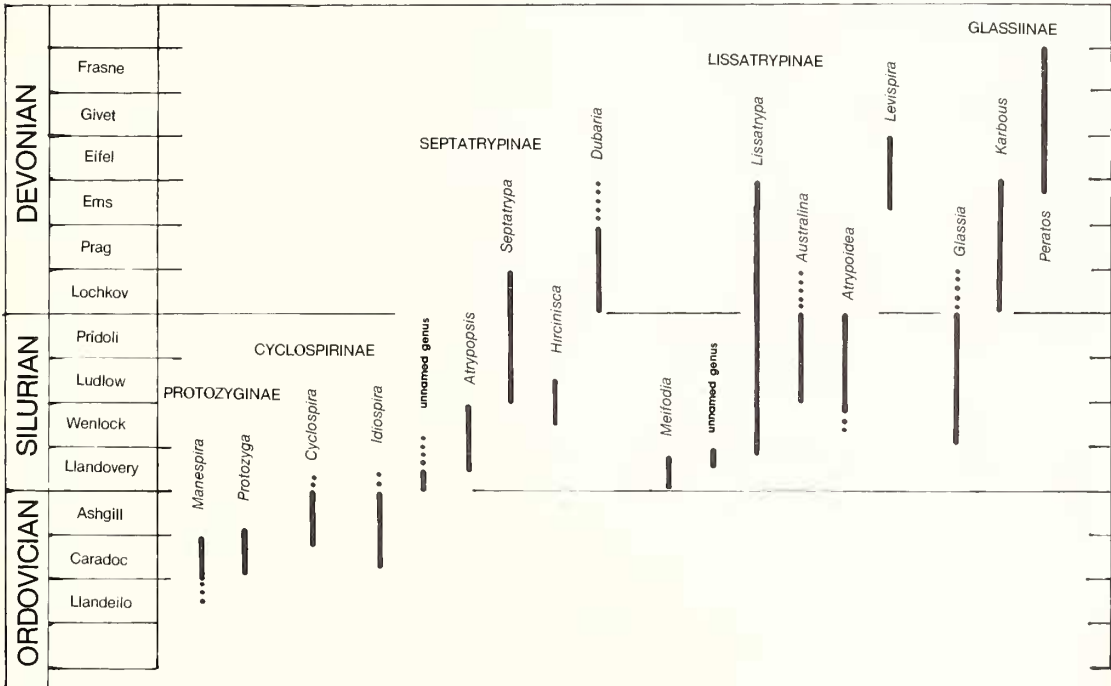
TEXT-FIG. 18. Stratigraphic distribution of known genera and subfamilies of smooth atrypoid brachiopods from Ordovician through Devonian time. The genera *Nanospira*, *Lissatrypoidea*, and *Tyrothyris* are taken as synonyms of *Australina*. *Buceqia* Havlicek and *Quangyuania* Sheng are interpreted as probable synonyms of *Lissatrypa*. *Cryptatatrypa* is a synonym of *Glassia*. The smooth brachiopod *Manosia* Zeng is a genus whose affinity is uncertain. The genus *Holynatrypa* is also of very uncertain status. Synonymous and dubious genera are not included in the range chart.

Remarks. This species is larger and less elongate than *Peratos beyrichi* (Kayser, 1872), of which a small collection was available for comparison, and *Glassia whidbornei* Davidson, 1882. Davidson was the first to figure the internal morphology of the genus correctly, i.e. the medially directed spiralia he demonstrated for *P. whidbornei.* However, he showed a fused jugum, which is not present in the two species examined. *Peratos arrectus* lacks the sulcus of *Glassia sulcata* (Siehl, 1962) and is substantially larger in size and with a more prominent beak than *Cryptatrypa philomela minor* Biernat 1966 or *Cryptatrypa hassiaca* Siehl, 1962. It is most similar in external form to *Terebratula newtoniensis* Davidson, 1867, but this is an even larger shell whose internal structure is unknown.

CONCLUSIONS

The diversity of the smooth atrypoids was at a peak during the Silurian, especially Wenlock–Ludlow time (text-fig. 18). Locally, smooth atrypoids such as *Meifodia, Lissatrypa, Atrypopsis, Septatrypa, Atrypoidea, Australina,* and *Glassia* were abundant enough to have formed thick coquinas, sometimes dominating to exclude other brachiopods. Such domination was very rare in the Devonian, when the group was in retreat, probably due to competition from the ribbed and frilly atrypoids. The last surviving group of smooth atrypoids, dying out in the Frasnian, was the Glassiinae, represented by the genus *Peratos,* which had medially directed spiralia similar to those with which the earliest atrypoids started in the Ordovician.

The spire-bearers probably first evolved about 470 Ma ago (Llandeilo), then saw relatively rapid evolution via a burst of diversification in Harnagian–Soudleyan times (CF7 to CF9). A second major burst occurred in the late Caradoc (late CF10 to CF11), some 455 Ma ago, with the expansion of the primitive smooth spire-bearers (*Idiospira* and *Cyclospira*) and ribbed spire-bearers (*Zygospira* and *Catazyga*). These earliest spire-bearers were then rapidly replaced during late Rawtheyan to Hirnantian times by the evolution of the Atrypidae, heralded by *Eospirigerina.* The Zygospiridae hung on as 'living fossils' during the latest Ordovician (CF13) and Llandoverian, to die out in Telychian (late Llandovery) time, except for the Tuvaellinae which persisted through to the late Silurian.

It is difficult to extend precise correlations between the brachiopod, graptolite and conodont zonations of the Caradoc and Ashgill. The conodont and graptolite zones tend to be of relatively long duration, for example, when compared to the upper Devonian. For the Upper Devonian, which lasted roughly 20 Ma, more than ten conodont zones exist. This compares unfavourably with the Upper Ordovician (Ashgill), which lasted about 19 Ma, and for which only two conodont zones are known. Brachiopods have the potential for a more precise dating scheme for Caradoc to Ashgill shelf carbonates and shales. The atrypoid spire-bearers show relatively rapid evolution at the genus level, and use for correlations at the species level.

At the Ordovician–Silurian boundary only two atrypoid genera, *Idiospira* and *Cyclospira,* may

---

Fig. 1. *Peratos arrectus* n. gen. and sp. Peel photograph of serially sectioned specimen demonstrating very thin dental plate and tissue lining the dental plate, dental cavity, deltidial plate (refer to text-fig. 17, section 1·2 mm), × 40.

Figs. 2, 7. *Glassia elongata* (Davidson, 1882). Peel photographs, × 40. 2, showing the presence of a very thin dental plate in the apical shell portions (arrow; see text-fig. 15, section at 0·6 mm). 7, showing the hinge plate structure with teeth in place and narrow crural bases (section at 1·4 mm).

Figs. 3–6. *Manespira nicolleti* (Winchell and Schuchert, 1892). Peel photographs, × 40. 3, 4, show the terminal points of the incomplete jugum (see text-fig. 7, section 2·9 mm). 5, 6, show the anterior portions of the jugum adjacent to their connection with the spiralium at 3·2 mm from the apex (see text-fig. 7). Scale × 40. Note the differences in the coarse calcite crystals which surround the ventral parts of the brachidia and the fine-grained surrounding matrix. This is common in all spire-bearers and appears to reflect the fact that early sediment infill preceded decay of the soft tissues.

PLATE 75
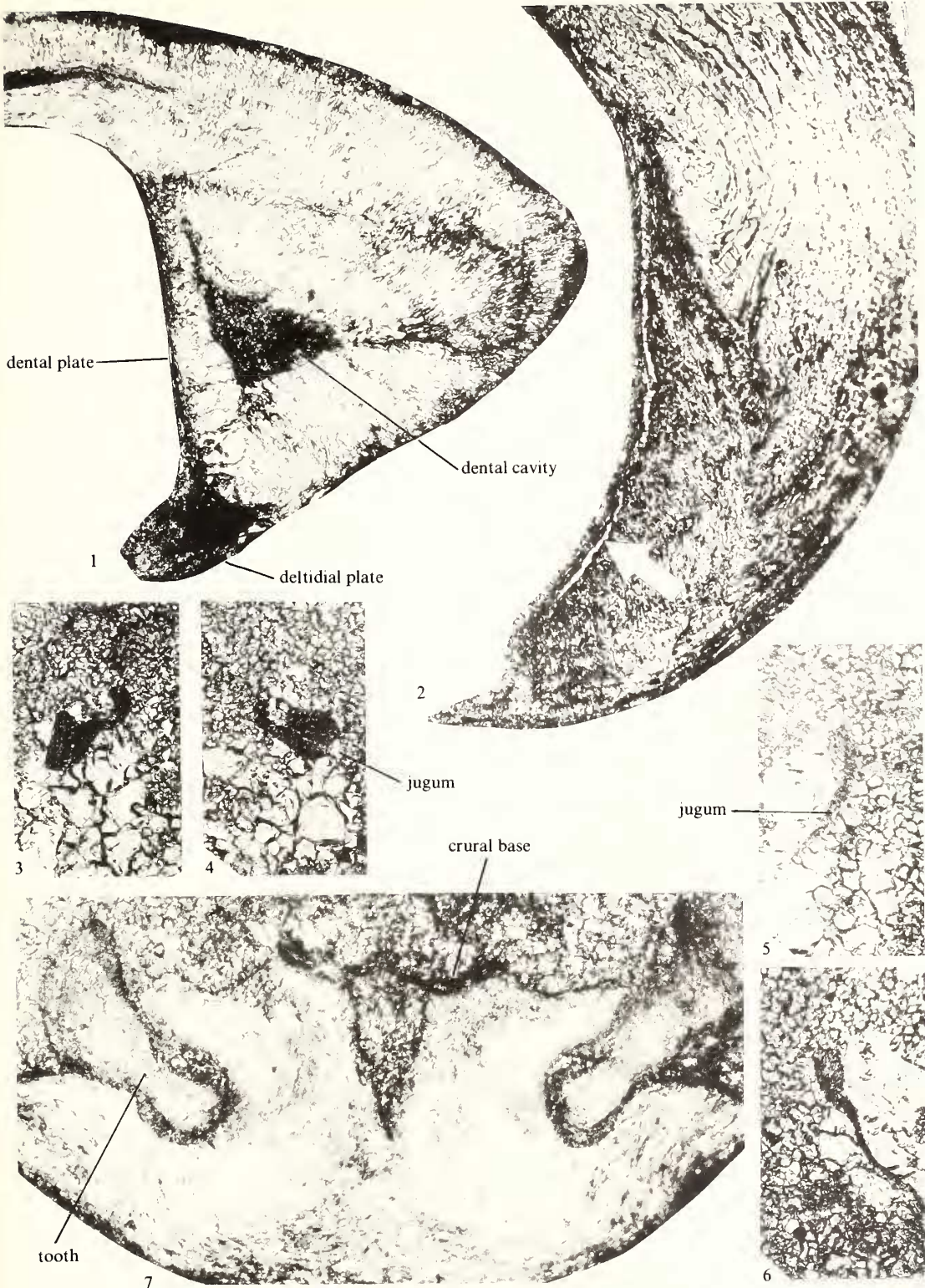
COPPER, atrypoid internal structures

have become extinct, and even these two have been reported (albeit here uncorroborated) from Silurian rocks. There is therefore no apparent major extinction of spire-bearing taxa at this boundary. The major decline and turn-over occurred during late Rawtheyan and/or early Hirnantian time, and this did not differ markedly from the late Caradoc turn-over. If late Ordovician glaciation did have an impact, it was at the CF12–CF13 (i.e. late Rawtheyan–early Hirnantian) boundary, which marks the introduction of strong 'Silurian' elements into the spire-bearer faunas, e.g. the appearance of *Hindella* (Meristellidae) and *Eospirigerina* (Atrypidae).

It should be noted that not all smooth atrypoids were necessarily derived monophyletically. A trend towards rib elimination and smoothing of the shell surface seems to be present in some genera of the Palaferellidae (e.g. *Gracianella, Prodavidsonia, Zeravshania, Eokarpinskia*) and Atrypidae (e.g. *Beitaia* Rong and Yang 1974, a very finely ribbed clintonellinid, is almost a homeomorph of *Septatrypa*; some *Spinatrypa* in the late Devonian have lost almost all ribs). The key to the evolutionary relationships of these secondarily derived 'smooth' genera, and other smooth brachiopods, must be internal structure, which is still unknown for more than ninety-five possible or probable species.

REFERENCES

AMSDEN, T. W. 1968. Articulate brachiopods of the St Clair Limestone (Silurian), Arkansas and the Clarita Formation (Silurian), Oklahoma. *Paleont. Soc. Mem.* **1**, 1–117.

BARRANDE, J. 1847. Ueber die Brachiopoden der silurischen Schichten von Böhmen. *Naturwissenschaftlichen Abhandlungen* 1(1). Braumüller und Seidel, Wien. 357–475.

—— 1879. *Système Silurien du centre de la Bohème, 1, Recherches paléontologiques, 5, Classe des mollusques, ordre de brachiopodes*, 226 pp. + atlas. Charles Bellmann, Prague.

BEECHER, C. E. and SCHUCHERT, C. 1893. Development of the brachial supports in *Dielasma* and *Zygospira*. *Proc. biol. Soc. Wash.* **8**, 71–82.

BERRY, W. B. N. 1976. Aspects of correlation of North American shelly and graptolitic faunas. *In* BASSETT, M. G. (ed.). *The Ordovician System*, 153–169. University of Wales Press and National Museum of Wales, Cardiff.

BIERNAT, G. 1966. Middle Devonian brachiopods of the Bodzentyn Syncline (Holy Cross Mountains). *Palaeontogr. polonica*, **17**, 1–162.

BILLINGS, E. 1859. Description of a new genus of Brachiopoda, and on the genus *Cyrtodonta*. *Can. Nat. Geologist*, **4**, 301–303.

—— 1863. Paleontology. *In* LOGAN, W. E. (ed.). Geology of Canada. *Geol. Surv. Can. Rep. Prog. 1863*, **9**, 136–197.

BOUCOT, A. J., JOHNSON, J. G. and STATON, R. D. 1964. On some atrypoid, retzioid and athyridoid Brachiopoda. *J. Paleont.* **38**, 805–822.

BOUCOT, A. J., JOHNSON, J. G., PITRAT, C. W. and STATON, R. D. 1965. Spiriferida. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology.* Part H. Brachiopoda. H632–H728. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas.

BRETSKY, P. W., BRETSKY, S. S. and SCHAEFER, P. J. 1977. Molluscan and brachiopod dominated biofacies in the Platteville Formation (Middle Ordovician), upper Mississippi Valley. *Bull. geol. Soc. Denmark*, **26**, 115–132.

CLARKE, J. M. 1913. Fosseis devonianos do Parana. *Monografias Div. geol. miner. Bras.* **1**, 1–353.

COCKS, L. R. M. 1978. A review of British Lower Palaeozoic brachiopods including a synoptic revision of Davidson's monograph. *Palaeontogr. Soc.* [*Monogr.*]. **131**, 1–356.

COOPER, G. A. 1956. Chazyan and related brachiopods. *Smithson. misc. Collns.* **127**, 1–1024 (plus atlas).
—— 1976. Early Middle Ordovician of United States. *In* BASSETT, M. G. (ed.). *The Ordovician System*, 1–696. University of Wales Press and National Museum of Wales, Cardiff.
—— and KINDLE, C. H. 1936. New brachiopods and trilobites from the Upper Ordovician of Percé, Quebec. *J. Paleont.* **10**, 348–372.
COPPER, P. 1967. Brachidial structures of some Devonian atrypid brachiopods. Ibid. **41**, 1176–1183.
—— 1973. *Bifida* and *Kayseria* (Brachiopoda) and their affinity. *Palaeontology*, **16**, 117–138.
—— 1977. *Zygospira* and some related Ordovician and Silurian atrypoid brachiopods. Ibid. **20**, 295–335.
—— 1978. Devonian atrypoids from western and northern Canada. *Spec. Pap. geol. Ass. Can.* **18**, 289–331.
—— 1982. Early Silurian atrypoids from Manitoulin Island and Bruce Peninsula, Ontario. *J. Paleont.* **56**, 68–702.
DAHMER, G. 1922. Studien über die Fauna des oberharzer Kahlebergsandsteins II. *Jb. preuss. geol. Landesanst.* **40**, 161–306.
DAVIDSON, T. 1865. A monograph of the British Fossil Brachiopoda, The Devonian Brachiopoda. *Palaeontogr. Soc. [Monogr.].* **6(1)**, 1–131.
—— 1869. A monograph of the British fossil Brachiopoda, The Silurian Brachiopoda. Ibid., **7(3)**, 169–248.
—— 1881a. On genera and species of spiral-bearing Brachiopoda, from specimens developed by the Rev. Norman Glass. *Geol. Mag.* **8(4)**, 1–12.
—— 1881b. Descriptions of new Upper Silurian Brachiopoda from Shropshire. *Geol. Mag.* **8(4)**, 145–156.
—— 1882. Supplement to the British Devonian Brachiopoda. *Palaeontogr. Soc. [Monogr.].* **5(1)**, 1–62.
—— 1883. Supplement to the British Silurian Brachiopoda. Ibid. 63–134.
DREVERMANN, F. 1901. Die Fauna des oberdevonischen Tuffbreccie von Langenaubach bei Haiger. *Jb. preuss. geol. Landesanst.* **21**, 99–207.
EMMONS, E. 1842. *Geology of New York, Part II, comprising the survey of the second geological district*, 437 pp. White and Visscher, Albany, New York.
—— 1855. *American geology, containing a statement of the principals of the science with full illustrations of the characteristic American fossils*, 251 pp. Sprague and Co., Albany, New York.
FOERSTE, A. F. 1893. Fossils of the Clinton Group in Ohio and Indiana. *Geol. Ohio*, **7**, 516–601.
—— 1914. The Rogers Gap fauna of central Kentucky. *J. Cincinn. Soc. nat. Hist.* **21**, 109–148.
FRECH, F. 1887. Ueber das Devon der Ostalpen, nebst Bemerkungen über das Silur und einem paläontologischen Abhang. *Z. dt. geol. Ges.* **39**, 659–728.
FU, LI-PU, 1982. Brachiopods. *In Paleontological atlas of Northwest China, Shaanxi-Gansu-Ningxia Volume, Part 1*, 95–179. Xian Inst. Geol. Miner. Resources, China.
GAGEL, C. 1890. Die Brachiopoden der cambrischen und silurischen Geschiebe im Diluvium der Provinzen Ost- und West Preussen. *Beitr. Naturk. preuss.* **6**, 1–79.
GARCIA-ALCALDE, J. L. 1973. Braquiopodos Devonicos de la Cordillera Cantabrica, 5, El aparato braquial de *Davidsonia* Bouchard-Chantereaux 1849 (Strophomenida-Davidsoniacea). *Breviora geol. astur.* **17**, 1–5.
GUNIA, T. 1962. Fauna of the limestone pebbles and the problem of the age of the Witoszow conglomerates (Lower Silesia). *Ann. Soc. geol. Pologne* **32**, 493–522.
—— 1968. On the fauna, stratigraphy and conditions of sedimentation of the Upper Devonian in the Swiebodicze depression (Middle Sudeten). *Geologica sudet.* **4**, 115–220.
HALL, J. 1847. Containing descriptions of the organic remains of the Lower Division of the New York System. *Rep. N.Y. St. Mus. nat. Hist.* 1–338.
—— 1852. Containing descriptions of the Lower Middle Division of the New York System. Ibid., 1–362.
—— and CLARKE, J. M. 1894. An introduction to the study of the genera of Palaeozoic Brachiopoda. *Rep. St. Geol. N.Y.* **13**, 601–943.
HAVLICEK, V. 1973. New brachiopod genera in the Devonian of Bohemia. *Vestn. ústr. Ust. geol.* **48**, 337–340.
—— 1984. *Bueeqia*, a new genus of the Lissatrypidae (Brachiopoda, Silurian). *Vestn. ústr. Ust. geol.* **59**, 109–110.
—— 1985. *Karbous*, g. n. (Lissatrypidae, Brachiopoda: Devonian) in Bohemia. *Vestn. ústr. Ust. geol.* **60**, 235–239.
—— and PLODOWSKI, G. 1974. Über die systematische Stellung der Gattung *Hircinisea* (Brachiopoda) aus dem böhmischen Ober-Silurium. *Senck. leth.* **55**, 229–249.
HEIDENHAIN, F. 1869. Ueber graptolithenführende Diluvial-Geschiebe der norddeutschen Ebene. *Z. dt. geol. Ges.* **21**, 143–182.
HERITSCH, F. 1929. Faunen aus dem Silur der Ostalpen. *Abh. geol. Bundesanst., Wien.* **23**, 1–183.

JAANUSSON, V. 1979. Ordovician. *In* TEICHERT, C. (ed.). *Treatise on invertebrate paleontology*. Part A, A136–A166. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas.

JOHNSON, J. G., BOUCOT, A. J. and MURPHY, M. A. 1976. Wenlockian and Ludlovian age brachiopods from the Roberts Mountain Formation of central Nevada. *Univ. Calif. Publs geol. Sci.* **115**, 1–102.

KAY, M. 1933. The Ordovician Trenton Group in northwestern New York; stratigraphy of the lower and upper limestone formations. *Am. J. Sci.* **26**, 1–15.

—— 1937. Stratigraphy of the Trenton Group. *Bull. geol. Soc. Am.* **48**, 233–302.

KAYSER, E. 1872. Studien aus dem Gebiete des rheinischen Devon, III, Die Fauna des Rotheisensteins von Brilon in Westfalen. *Z. dt. geol. Ges.* **24**, 653–690.

KULKOV, N. P. 1974. Brachiopods. *In* Rugosans, brachiopods and stratigraphy of the Silurian of the Altai-Sayan mountain region. *Trudy Inst. Geol. Geofiz. sib. Otd.* **231**, 1–121. [In Russian.]

KUNTH, A. 1865. Die lösen Versteinerungen im Diluvium von Tempelhof bei Berlin. *Z. dt. geol. Ges.* **17**, 311–332.

LENZ, A. C. 1970. Late Silurian brachiopods of Prongs Creek, northern Yukon. *J. Paleont.* **44**, 480–500.

—— 1977*a*. Upper Silurian and Lower Devonian brachiopods of Royal Creek, Yukon, Canada. *Palaeontographica* A**159**, 111–138.

—— 1977*b*. Llandoverian and Wenlockian brachiopods from the Canadian Cordillera. *Can. J. Earth. Sci.* **14**, 1521–1554.

LIBERTY, B. A. 1971. Paleozoic geology of Wolfe Island, Bath, Sydenham and Gananoque map-areas, Ontario. *Geol. Surv. Pap. Can.* **70-35**, 1–12.

LIU DIYONG, ZHANG ZIXIN and DI QIAOLING. 1984. Middle Ordovician brachiopods from Mts. Kunlun and Altun. *Acta Palaeont. Sin.* **23**, 155–169.

LOCKLEY, M. G. 1980. The Caradoc faunal associations of the area between Bala and Dinas Mawddwy, north Wales. *Bull. Br. Mus. nat. Hist.* (Geol.) **33**, 167–235.

M'COY, F. 1851. On some new Cambro-Silurian fossils. *Ann. Mag. nat. Hist.* **8**, 387–409.

—— 1855. A systematic description of the British Palaeozoic fossils. *In* SEDGWICK, A. and M'COY, F., *A synopsis of the classification of the British Palaeozoic rocks*, 661 pp. J. W. Parker, West Strand, London.

MACKINNON, D. I. The shell structure of spiriferide Brachiopoda. *Bull. Brit. Mus. nat. Hist.* (Geol.). **25**, 189–261.

MAILLEUX, E. 1936. La faune des schistes de Matagne. *Mém. Inst. r. Sci. nat. Belg.* **77**, 1–75.

MAURER, F. 1881. Paläontologischen Studien im Gebiet des rheinischen Devon, 4, Der Kalk bei Greifenstein. *Neues Jb. Miner. Geol. Paläont.* 1, 1–112.

—— 1885. *Die Fauna des Kalkes von Waldgirmes bei Giessen*, 340 pp. Bergstrasser, Darmstadt.

MENAKOVA, G. N. 1983. Zeravshania—a new Paleozoic brachiopod genus from central Tadzhikistan. *Paleont. Zh.* **1983(1)**, 66–73.

MEYER, H. V. and MÜNSTER, G. G. 1840. Die Versteinerungen des Uebergangskalkes mit Clymenien und Orthoceratiten von Oberfranken. *Beitr. Petrefactenkunde*, 3, 33–121.

MITCHELL, W. I. 1977. The Ordovician Brachiopoda from Pomeroy, Co. Tyrone. *Palaeontrog. Soc.* [*Monogr.*]. **130**, 1–138.

NIKIFOROVA, O. I. 1937. Faunal characteristics of the Upper Silurian of western Pribalkhash. *Tsent. nauchno-issled. geol. Razv. Inst.* (*TSNIGRI*), 11–36. [In Russian.]

—— 1941. Some brachiopods of the upper Silurian from the Kheta and Khandyga river basins (Siberia). *Trudy arkt. nauchno-issled. Inst.* **158**, 103–120.

—— 1961. Paleontology. *In* NIKIFOROVA, O. I. and ANDREEVA, A. N. Stratigraphy of the Ordovician and Silurian of the Siberian Platform and its paleontological basis. *Trudy Vses. nauchno-issled. geol. Inst.* (*VSEGEI*). **1**, 67–290. [In Russian.]

—— and MODZALEVSKAYA, T. L. 1968. Some Llandoverian and Wenlockian brachiopods from the northwest part of the Siberian Platform. *Uchen. Zap. nauchno-issled. Inst. geol. Arkt.* **21**, 50–81. [In Russian.]

PARKS, W. A. 1915. Palaeozoic fossils from a region southwest of Hudson Bay. *Trans. r. Can. Inst.* **11**, 1–95.

PERRY, D. G. 1985. Brachiopoda and biostratigraphy of the Siluro-Devonian Delorme Formation in the District of Mackenzie. *Contr. r. Ont. Mus.* **138**, 1–243.

RAYMOND, P. E. 1911. The Brachiopoda and Ostracoda of the Chazy. *Ann. Carneg. Mus.* **7**, 215–259.

REED, F. R. C. 1897. The fauna of the Keisley Limestone, II. *Q. Jl geol. Soc. Lond.* **53**, 67–106.

—— 1917. The Ordovician and Silurian Brachiopoda of the Girvan District. *Trans. r. Soc. Edinb.* **51**, 795–998.

—— 1936. The lower Palaeozoic faunas of the Southern Shan states. *Mem. geol. Surv. India*, **21**, 1–183.

ROEMER, F. 1885. Lethaia erratica oder Aufzahlung und Beschreibung der norddeutschen Ebene vorkommenden Diluvial-Geschiebe nordischer Sedimentär-Gesteine. *Paläont. Abh.* **5**, 1–173.

RONG JIAYU, XU HANKUI and YANG XUECHANG. 1974. Silurian brachiopods, 195–208. *In Handbook of stratigraphy and palaeontology of SW China*, 454 pp. Academy of Science, Nanjing. [In Chinese.]

ROY, S. K. 1941. The Upper Ordovician fauna of Frobisher Bay, Baffin Island. *Mem. Field. Mus. nat. Hist.* **2**, 1–212.

ROOMUSOKS, A. 1964. Some brachiopods from the Ordovician of Estonia. *Tartu Ulik. Geol.-Inst. Toim.* **153**, 3–28.

ROZMAN, K. S. 1964. Middle and Late Ordovician brachiopods of the Selennyakh range. *Trudy Inst. geol. Nauk, Mos.* **106**, 106–204.

—— 1968. Brachiopods of the Selennyakh and Sette-Daban mountain ranges. *In* BALASHOV, E. G. (ed.). *Field atlas of the Ordovician fauna of NE USSR*. 53–76. Akad. Nauk Moskva.

RUBEL, M. 1977. Revision of dayiacean brachiopods from the Silurian of the NE Baltic. *Geol.-Inst. Toim.* **26**, 211–220.

RUDWICK, M. J. S. 1960. The feeding mechanisms of spire-bearing fossil brachiopods. *Geol. Mag.* **97**, 369–383.

RYBNIKOVA, M. V. 1967. Brachiopoda. *In* GALITE, L. K. *et al., Stratigraphy, fauna, and environmental conditions of the Silurian rocks of the central Baltic*, 304 pp. Minist. Geol. SSSR Inst. Geol. Riga. [In Russian.]

RZHONSNITSKAYA, M. A. 1960. Order Atrypida. *In* ORLOV, Y. A. (ed.). *Osnovy paleontologii: Bryozoa and Brachiopoda*, 1–343. Nedra Press, Moskva. [In Russian.]

—— 1964. On Devonian atrypids of the Kuznetsk Basin. *Paleontologiya i stratigrafiya, Trudy Vses. nauchnoissled. geol. Inst.* **93**, 91–112.

SALTER, J. W. 1873. *A catalogue of the collection of Cambrian and Silurian fossils contained in the geological museum of the university of Cambridge*, 204 pp. Cambridge University Press, Cambridge.

SAMTLEBEN, C. 1972. Feinbau und Wachstum von Spiriferiden-Armgerüsten. *Paläont. Z.* **46**, 20–33.

SARDESON, F. W. 1892. The range and distribution of the Lower Silurian fauna of Minnesota with descriptions of some new species. *Bull. Minn. Acad. nat. Sci.* **3**, 326–343.

SCHUCHERT, C. 1894. A revised classification of the spire-bearing Brachiopoda. *Am. Geol.* **13**, 102–107.

—— and COOPER, G. A. 1930. Upper Ordovician and Lower Devonian stratigraphy and paleontology of Percé, Quebec. *Am. J. Sci.* **20**, 162–288.

SHENG HUAIBIEN. 1975. Silurian *Atrypella* from Quangyuan, Sichuan. *Prof. Pap. Strat. Paleont.* **2**, 78–79. [In Chinese.]

SIEHL, A. 1962. Der Greifensteinerkalk (Eiflium, Rheinisches Schiefergebirge) und seine Brachiopodenfauna. *Palaeontographica* **A119**, 173–221.

SOWERBY, J. de C. 1839. Organic remains. *In* MURCHISON, R. I., *The Silurian System*, 579–712. John Murray.

SPRIESTERSBACH, J. and FUCHS, A. 1909. Die Fauna der Remscheiderschichten. *Abhandl. preuss. geol. Landesanst.* **58**, 1–81.

STRUSZ, D. L. 1982a. On *Australina* Clarke and its junior synonyms *Lissatrypa, Lissatrypoidea,* and *Tyrothyris* (Silurian–Devonian Brachiopoda). *J. Aust. Geol. Geophys.* **7**, 73–77.

—— 1982b. Wenlock brachiopods from Canberra, Australia. *Alcheringa,* **6**, 105–142.

SU YANGZHENG. 1977. Cambro-Devonian Brachiopoda. *In Paleontological atlas of northeast China,* 254–327. Shenyang Institute of Geology and Mineral Resources, Geol. Publ. House, Beijing. [In Chinese.]

SWEET, W. C. and BERGSTRÖM, S. M. 1976. Conodont biostratigraphy of the Middle and Upper Ordovician of the United States midcontinent. *In* BASSETT, M. G. (ed.). *The Ordovician System,* 121–152. University of Wales Press and National Museum of Wales, Cardiff.

TEMPLE, J. T. 1968. The lower Llandovery (Silurian) brachiopods from Keisley, Westmorland. *Palaeontogr. Soc.* [*Monogr.*]. **122**, 1–58.

TIETZE, E. 1871. Ueber die devonischen Schichten von Ebersdorf umweit Neurode in der Grafschaft Glatz, eine geognostisch-paläontologische Monographie. *Palaeontographica,* **19**, 103–158.

TITUS, R. and CAMERON, B. 1976. Fossil communities of the lower Trenton Group (Middle Ordovician) of central and northwestern New York state. *J. Paleont.* **50**, 1209–1225.

TORLEY, K. 1934. Die Brachiopoden des Massenkalkes der oberen Givetstufe von Bilveringsen bei Iserlohn. *Abh. senckenb. naturforsch. Ges.* **43**, 67–148.

TWENHOFEL, W. H. 1914. The Anticosti Island faunas. *Mus. Bull. Can. geol. Surv.* **3**, 1–35.

VENYUKOV, P. N. 1899. Die Fauna der silurischen Ablagerungen des Gouvernements Podolien. *Mater. Geol. Ross.* **19**, 21–266.

VLADIMIRSKAYA, Y. V. 1972. Systematic position and geologic range of the genus *Tuvaella* (Brachiopoda). *Paleont. Z.* **1972**(1), 37–44.

WELLER, S. 1903. The Paleozoic faunas. *Rep. geol. surv. New Jers.* **3**, 1–462.

WHITEAVES, J. F. 1904. Preliminary list of fossils from the Silurian (Upper Silurian) rocks of the Ekwan River and Sutton Mill lakes, Keewatin. *Ann. Rep. geol. Surv. Can.* **14** (F), 38–59.

—— 1906. The fossils of the Silurian (Upper Silurian) rocks of Keewatin, Manitoba, the northeastern shore of Lake Winnipegosis and the lower Saskatchewan river. *Rep. geol. Surv. Can. Palaeozoic Fossils.* **8**, 243–298.

WILLIAMS, A. 1951. Llandovery brachiopods from Wales with special reference to the Llandovery District. *Q. Jl geol. soc. Lond.* **107**, 85–136.

—— 1962. The Barr and Lower Ardmillan Series (Caradoc) of the Girvan District, southwest Ayrshire, with descriptions of the Brachiopoda. *Mem. geol. Soc. Lond.* **3**, 1–267.

—— and HURST, J. 1977. Brachiopod evolution. *Dev. Paleont. Strat.* **5**, 79–121.

—— and WRIGHT, A. D. 1961. The origin of the loop in articulate brachiopods. *Palaeontology*, **4**, 149–176.

WILSON, A. E. 1932a. Ordovician fossils from the region of Cornwall, Ontario. *Trans. r. Soc. Can.* 3(26), 373–404.

—— 1932b. Palaeontological notes. *Can. Fld Nat.* **46**, 133–140.

—— 1946. Brachiopoda of the Ottawa Formation of the Ottawa–St. Lawrence Lowland. *Bull. geol. Surv. Can.* **8**, 1–149.

WINCHELL, N. H. and SHUCHERT, C. 1892. Preliminary descriptions of new Brachiopoda from the Trenton and Hudson River groups of Minnesota. *Am. Geol.* **9**, 284–294.

—— 1893. The Lower Silurian Brachiopoda of Minnesota. *Geology of Minnesota*, **3**, 333–474.

WRIGHT, A. D. 1979. The origin of the spiriferidine brachiopods. *Lethaia*, **12**, 29–33.

XU HANKUI. 1979a. Brachiopoda. *In Paleontological atlas of northwestern China. 1, Qinghai,* 60–112. Beijing Geological Publishing House, China.

—— 1979b. Brachiopods from the Tangxiang Formation (Devonian) in Nandan, Guangxi. *Acta Paleont. Sin.* **18**, 362–380.

ZENG QINGLUAN. 1983. Latest Ordovician and early Silurian faunas from the eastern Yangtze Gorges, China, with comments on the Ordovician–Silurian boundary. *Bull. Yichang Inst. Geol. Min. Res.* **6**, 95–127.

PAUL COPPER

Department of Geology
Laurentian University
Sudbury, Ontario
Canada P3E 2C6

NOTE ADDED IN PROOF

After this manuscript went to press, three further papers, citing new genera, species, or revised designations, were received. These are relevant to the data presented:

Terebratula turjensis Gruenewaldt, 1854, pl. 2, fig. 8a–d. Emsian–Eifelian beds, eastern slopes of the Urals, USSR. Mizens (1984) relegates this to the genus *Holynatrypa*, but serial sections provided indicate this is probably the glassiid genus *Karbous* Havlicek.

Lissatrypella Sapelnikov and Mizens, 1982 (type *Atrypa kuschvensis* Chernyshev, 1893), Upper Wenlock to Pridoli, Urals and Central Asia. This is like the genus *Atrypoidea* but has a wide anterior fold giving a resemblance to some *Septatrypa*. It may be more suitable to regard this as a subgenus variant of *Atrypoidea* considering the variation in development of the anterior fold.

Lissatrypa (Nanatrypa) Sapelnikov and Mizens, 1982 (type *Atrypa canaliculatiformis* Chernyshev, 1893), Wenlock–Ludlow, eastern Urals, USSR. This is a subgenus with a marked sulcus on both valves. No internal structures are shown, but there is a strong similarity to the bisinuosity seen in many *Glassia*, to which it may possibly be assigned if spiralia are shown to be medially directed.

Anlidospira chuxianensis Liu, 1983, p. 285, pl. 93, figs. 15–16. Tangtao Formation, Upper Ordovician, Zhe County, Anhui Province, China. Liu diagnoses this species with a convex horizontal, ventral platform. No internal illustrations are shown and this species is tentatively assigned to *Cyclospira*.

REFERENCES

CHERNYSHEV, T. 1893. Die Fauna des unteren Devon am Ostabhange des Ural. *Trudy Geol. Kom.* 4(3), 1–221.
GRUENEWALDT, M. V. 1854. Ueber die Versteinerungen des silurischen Kalke von Bogosslowsk. Ein Beitrag zur Geologie des oestlichen Ural. *Mém. Savants Étrang.* 7, 571–620.
LIU DIYONG, XU HANKUI and LIANG WANGPING. 1983. Brachiopoda. *In Paleontological atlas of east China*, 254–286. Beijing Geological Publishing House, China. [In Chinese.]
MIZENS, L. I. 1984. Lower Devonian and Eifelian atrypids from the eastern slopes of the Urals. *Akad. Nauk SSSR, Uralskii Nauchnyi Tsentr*, 1–111.
SAPELNIKOV, V. P. and MIZENS, L. I. 1982. Smooth Silurian atrypoids from the eastern slopes of the Central and Northern Urals. Ibid. 1–51. [In Russian, labelled 'preprint'.]

ERRATUM

Palaeontology, Vol. 29, Part 2, 1986, p. 303:

The senior author's name should read Malinky *not* Malinkey.